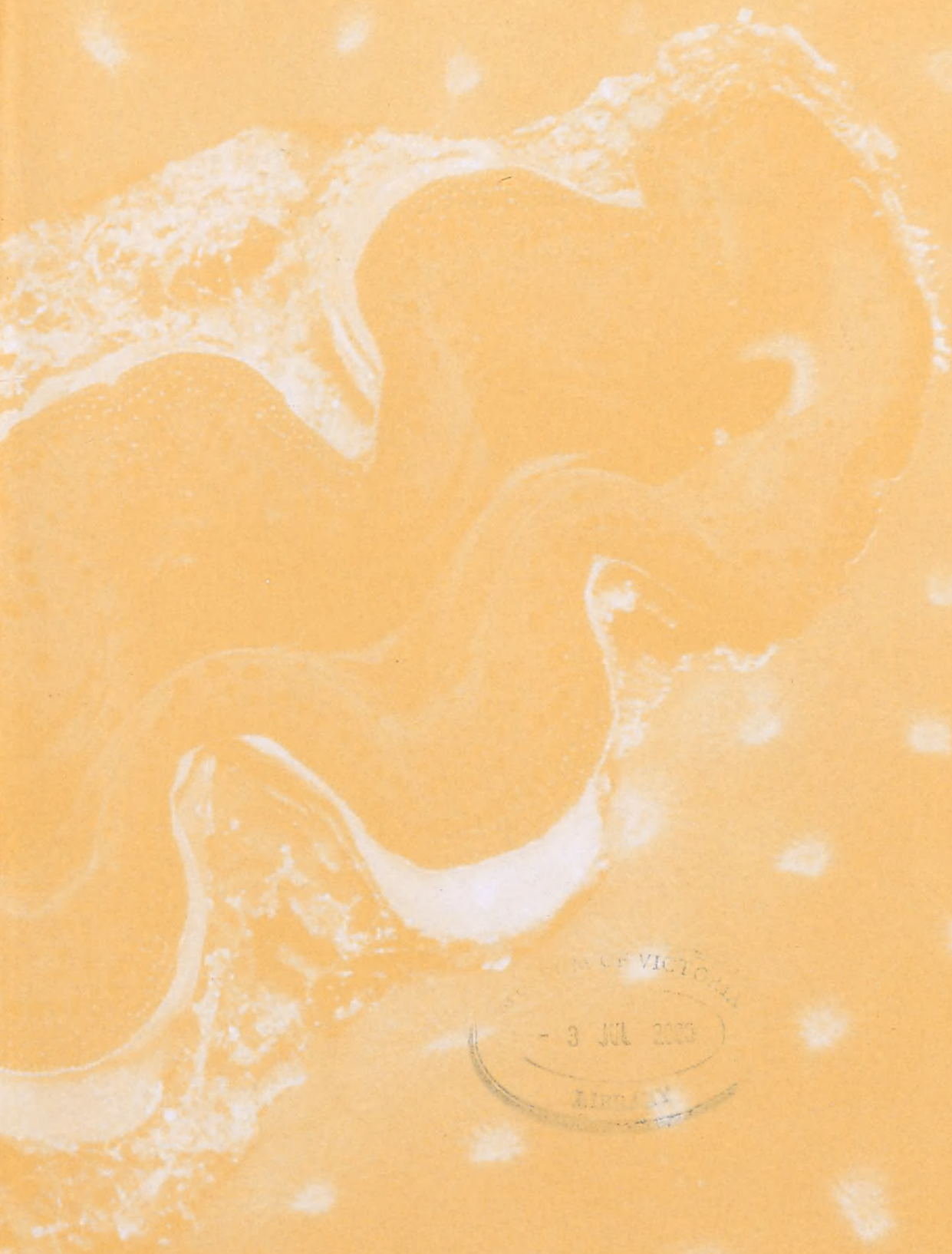




MOLLUSCA

The Southern Synthesis





~~Info Zone~~

MOLLUSCA

The Southern Synthesis

Australian Biological Resources Study, Canberra

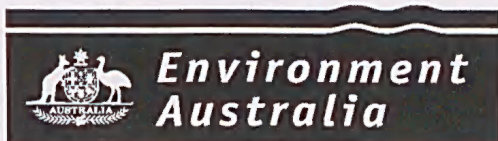


MOLLUSCA

The Southern Synthesis

Part B

Fauna of Australia Volume 5



Department of the Environment



This work is copyright. Apart from any use as permitted under the *Copyright Act 1968*, no part may be reproduced by any process or stored in any retrieval system or database without prior written permission from the copyright holder. Requests and inquiries concerning reproduction and rights should be addressed to the Director, Australian Biological Resources Study, GPO Box 636, Canberra, ACT 2601, Australia.

EDITORIAL COMMITTEE

Professor R.E. Jones (Chairman)
Dr I. Beveridge
Dr L.R.G. Cannon
Dr M.S. Harvey
Dr E.S. Nielsen
Dr W.F. Ponder
Dr J. Just (Director, Fauna, *ex officio*)

SERIES MANAGER

Graham J.B. Ross

VOLUME EDITORS

Pamela L. Beesley
Graham J.B. Ross
Alice Wells

GRAPHIC DESIGNER

Isabel Hallam

TECHNICAL ASSISTANCE

Winston F. Ponder
A.J. Underwood
Fred E. Wells

This work may be cited as:

Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) (1998). *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5.* CSIRO Publishing : Melbourne, Part A xvi 563 pp. Part B viii 565–1234 pp.

A chapter may be cited as:

Morton, B. Prezant, R.S. & Wilson, B. (1998). Class Bivalvia. Pp. 195–234 in Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5.* CSIRO Publishing : Melbourne, Part A xvi 563 pp.

An introduction in a chapter may be cited as:

Fretter, V., Graham, A., Ponder, W.F. & Lindberg, D.L. (1998). Prosobranchia Introduction. Pp. 605–638 in Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5.* CSIRO Publishing : Melbourne, Part B viii 565–1234 pp.

A taxon in a chapter may be cited as:

Haszprunar, G. (1998). Superorder Cocculiniformia. Pp. 653–664 in Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5.* CSIRO Publishing : Melbourne, Part B viii 565–1234 pp.

National Library of Australia Cataloguing-in-Publication entry

Mollusca: The Southern Synthesis
Mollusca
Includes bibliographies and index
ISBN 0 643 05756 0
1. Zoology - Australia.
2. Mollusca - Australia.
I. Australian Biological Resources Study.
II. Title: Mollusca: The Southern Synthesis.
591.994

This book is available from:

CSIRO PUBLISHING
PO Box 1139 (150 Oxford Street)
Collingwood VIC 3066
Australia

Tel: (03) 9662 7666 Int: +(61 3) 9662 7666
Fax: (03) 9662 7555 Int: +(61 3) 9662 7555
Email: sales@publish.csiro.au

Endpapers. Like a jewel in a star-studded sky, an embedded giant clam, *Tridacna crocea*, displays its mantle to the light, used by symbiotic algae to photosynthesise nutrients shared with their host. [L. Newman & A. Flowers]

Plates 7-37, background. The superabundant cardiid *Fragum erugatum*, the primary component of Shell Beach, Shark Bay, Western Australia. [M. Fagg]

CONTENTS

PART A

Preface	v
Contributors	vii
Authors' Contributions	xi

1	Phylum MOLLUSCA	1
2	Class APLACOPHORA	145
3	Class POLYPLACOPHORA	161
4	Class BIVALVIA	195
5	Subclass PROTOBRANCHIA	235
6	Subclass PTERIOMORPHIA	249
7	Subclass PALAEOHETERODONTA	289
8	Subclass HETERODONTA	301
9	Subclass ANOMALODESMATA	397
10	Class SCAPHOPODA	431
11	Class CEPHALOPODA	451
12	Subclass NAUTILOIDEA	485
13	Subclass COLEOIDEA	499

PART B

Authors' Contributions	vi
Class GASTROPODA	565
PROSOBRANCHS	605
OPISTHOBRANCHIA	915
PULMONATA	1037
Glossary	1127
Index	1147

AUTHORS' CONTRIBUTIONS

Authors' contributions are listed here with page numbers as a ready source of reference for purposes of citation. Its primary purpose is to ensure that authors receive due recognition for their contribution. Examples of citations covering four different levels are provided on page iv.

PART A

1 Phylum MOLLUSCA

1-144

Definition and General Description by DON T. ANDERSON	1
Classification of Mollusca by WINSTON F. PONDER	1-6
History of Discovery by J. HOPE BLACK	6-11
Morphology and Physiology of the Mollusca by BRONWEN J. SCOTT & RON KENNY	11-23
Molluscan Life Histories by COLIN LITTLE	23-29
Molluscs on Rocky Shores by A.J. UNDERWOOD	29-32
Molluscs on Coral Reefs by CARLA CATTERALL	33-36
Molluscs in Marine and Estuarine Sediments by CHARLES H. PETERSON & FRED E. WELLS	36-46
Pelagic Molluscs by RUDOLF S. SCHELTEMA, LESLIE NEWMAN & LU CHUNG CHENG	46-55
<i>Holopelagic Gastropods</i> by Leslie Newman	
<i>Cephalopods</i> by Lu Chung Cheng	
<i>Meroplankton</i> by Rudolf S. Scheltema	
Molluscs on Land by COLIN LITTLE	55-59
Molluscs of Inland Waters by KEITH F. WALKER	59-65
Economic Significance by JOE BORAY & JOHN L. MUNRO	65-77
<i>Molluscs and Parasitic Diseases, Molluscs as Plant Pests</i> by Joe Boray	
<i>Fisheries and Mariculture</i> by John L. Munro	
Distribution and Relationships of Marine and Estuarine Fauna by WINSTON F. PONDER & FRED E. WELLS	77-80
Distribution and Affinities of Non-Marine Molluscs by WINSTON F. PONDER, FRED E. WELLS & ALAN SOLEM	80-88
<i>Non-Marine Zoogeographical Regions</i> by Fred E. Wells	
<i>The Freshwater Molluscan Fauna</i> by Winston F. Ponder	
<i>The Terrestrial Molluscan Fauna</i> by Alan Solem	
The Fossil Record by PETER A. JELL & THOMAS A. DARRAGH	88-101
<i>Introduction</i> by Peter A. Jell & Thomas A. Darragh	
<i>Palaeozoic Era, Mesozoic Era</i> by Peter A. Jell	
<i>Cainozoic Era</i> by Thomas A. Darragh	
Methods and Techniques in Malacology by WINSTON F. PONDER	101-104
Quantitative Ecological Sampling of Molluscs by A.J. UNDERWOOD	104-105
Conservation by WINSTON F. PONDER	105-115

2 Class APLACOPHORA

145-159

by AMÉLIE H. SCHELTEMA

3 Class POLYPLACOPHORA

161-194

Introduction by PIET KAAS, ALLAN M. JONES & KAREN L. GOWLETT-HOLMES	161-177
<i>Definition and General Description, History of Discovery, Morphology and Physiology, Natural History (Life History, Ecology and Behaviour, Economic Significance), Classification</i> by Piet Kaas & Allan M. Jones	
<i>Natural History (Biogeography), Fossil Record</i> by Karen L. Gowlett-Holmes	

Suborder Lepidopleurina by PIET KAAS	178
Family Lepidopleuridae by KAREN L. GOWLETT-HOLMES	178-179
Family Hanleyidae by KAREN L. GOWLETT-HOLMES	179-180
Suborder Chorioplacina by KAREN L. GOWLETT-HOLMES	180
Family Chorioplacidae by KAREN L. GOWLETT-HOLMES	180
Suborder Ischnochitonina by PIET KAAS	180
Family Ischnochitonidae by TONIA COCHRAN	180-183
Family Schizochitonidae by KAREN L. GOWLETT-HOLMES	183-184
Family Mopaliidae by KAREN L. GOWLETT-HOLMES	184-185
Family Chitonidae by KAREN L. GOWLETT-HOLMES	185-188
Suborder Acanthochitonina by PIET KAAS	188
Family Acanthochitonidae by KAREN L. GOWLETT-HOLMES	188-189
Family Cryptoplacidae by KAREN L. GOWLETT-HOLMES	189

4 Class BIVALVIA

195-234

by BRIAN MORTON, ROBERT S. PREZANT & BARRY WILSON

*Definition and General Description, Morphology and Physiology
(External Features and Shells), Biogeography, Fossil History and
Phylogeny, Classification* by Robert S. Prezant
*History of Discovery, Morphology and Physiology (Mantle and
Body Cavities, Musculature and Locomotion, Feeding and
Digestion, Excretion, Respiration, Sense Organs and Nervous
System, Reproduction, Embryology), Natural History*
by Brian Morton
Barry Wilson revised the chapter and added Australian material

5 Subclass PROTOBRANCHIA

235-247

by ROBERT G.B. REID

6 Subclass PTERIOMORPHIA

249-288

Introduction by BARRY WILSON	249-250
Order Mytiloida by BARRY WILSON	250-253
Order Arcoida by SUZANNE E. BOYD	253-261
Order Pteroida by ALAN J. BUTLER	261-267
Order Limoida by ALAN J. BUTLER	267-268
Order Ostreoida by SHIRLEY M. SLACK-SMITH	268-282

7 Subclass PALAEOHETERODONTA

289-300

Introduction by ROBERT S. PREZANT	289-294
Order Trigonoida by THOMAS A. DARRAGH	294-296
Order Unionoida by BRIAN J. SMITH	296-298

8 Subclass HETERODONTA

301-396

Introduction by ROBERT S. PREZANT	301-307
Order Veneroida by BRIAN J. SMITH	306-307
Superfamily Chamoidea by SHIRLEY M. SLACK-SMITH	307-309
Superfamily Lucinoidea by ROBERT G.B. REID & SHIRLEY M. SLACK-SMITH	309-315
Superfamily Galeommatoidea by WINSTON F. PONDER	316-318
Superfamily Cyamioidea by WINSTON F. PONDER & ROGER G. DE KEYZER	318-322

Superfamily Carditoidea by SHIRLEY M. SLACK-SMITH	322–325
Superfamily Crassatelloidea by SHIRLEY M. SLACK-SMITH	325–328
Superfamily Cardioidea by BARRY WILSON	328–332
Superfamily Tridacnoidea by RICHARD BRALEY & JOHN M. HEALY	332–336
Superfamily Mactroidea by JOHN M. HEALY & KEVIN LAMPRELL	336–340
Superfamily Solenoidea by RICHARD C. WILLAN	340–341
Superfamily Tellinoidea by RICHARD C. WILLAN	342–348
Superfamily Arcticoidea by SHIRLEY M. SLACK-SMITH	348–351
Superfamily Glossoidea by SHIRLEY M. SLACK-SMITH	351–352
Superfamily Corbiculoidea by DAVID J. BRUNCKHORST	352–355
Superfamily Veneroidea by MARY E. HARTE	355–362
Order Myoida by BARRY WILSON	362–363
Superfamily Myoidea by KEVIN LAMPRELL, JOHN M. HEALY & GEOFFREY R. DYNE	363–366
Superfamily Gastrochaenoidea by KARL H. KLEEMANN	367–370
Superfamily Hiatelloidea by DAVID J. BRUNCKHORST	370–371
Superfamily Pholadoidea by RUTH D. TURNER	371–378

9
Subclass ANOMALODESMATA
397–429

Introduction by ROBERT S. PREZANT	397–405
Superfamily Pholadomyoidea by ROBERT S. PREZANT	405–407
Superfamily Thracioidea by ROBERT S. PREZANT	407–412
Superfamily Clavagelloidea by BRIAN J. SMITH	412–415
Superfamily Pandoroidea by ROBERT S. PREZANT	415–420
Superfamily Verticordioidea by ROBERT S. PREZANT	420–422
Superfamily Poromyoidea by ROBERT S. PREZANT	422–424
Superfamily Cuspidarioidea by ROBERT S. PREZANT	424–425

10
Class SCAPHOPODA
431–450

Introduction by C.P. PALMÉR & GERHARD STEINER	431–438
Order Dentaliida by GERHARD STEINER	439–443
Order Gadilida by GERHARD STEINER	443–447

11
Class CEPHALOPODA
451–484

by KATHARINA MANGOLD, MALCOLM R. CLARKE & CLYDE F.E. ROPER	
<i>Economic Significance by Clyde F.E. Roper, all other text by Katharina Mangold & Malcolm R. Clarke</i>	

12
Subclass NAUTILOIDEA
485–498

Introduction and Fossil Record by MARY WADE & BRIAN STAIT	485–493
Family Nautilidae by WILLIAM B. SAUNDERS	494–496

13
Subclass COLEOIDEA
499–563

Introduction by LU CHUNG CHENG & MALCOLM C. DUNNING	499–503
<i>Reproduction and Economic Significance by Malcolm C. Dunning all other text by Lu Chung Cheng</i>	
Order Sepioidea by LU CHUNG CHENG	504–514
Order Teuthoidea by MALCOLM C. DUNNING & LU CHUNG CHENG	515–542
Order Vamyromorpha by LU CHUNG CHENG	542–545
Order Octopoda by LU CHUNG CHENG	545–554

PART B

14
Class GASTROPODA
565–604

by E. ALISON KAY, FRED E. WELLS & WINSTON F. PONDER	
<i>Classification by Winston F. Ponder, all other text by E. Alison Kay & Fred E. Wells</i>	

15
PROSOBRANCHS
605–913

Introduction by VERA FRETTER, ALASTAIR GRAHAM, WINSTON F. PONDER & DAVID R. LINDBERG	605–638
Subclass Eogastropoda by WINSTON F. PONDER	639
Order Patellogastropoda by DAVID R. LINDBERG	639–652
Subclass Orthogastropoda by WINSTON F. PONDER	652
Superorder Cocculiniformia by GERHARD HASZPRUNAR	653–664
Superorder Vetigastropoda by WINSTON F. PONDER	664
Superfamily Pleurotomarioidea by CAROLE S. HICKMAN	664–669
Superfamily Fissurelloidea by CAROLE S. HICKMAN	669–671
Superfamily Trochoidea by CAROLE S. HICKMAN	671–692
Superfamily Seguenzioidea by CAROLE S. HICKMAN	692–693
Superorder Neritopsina by WINSTON F. PONDER	693–694
Superfamily Neritoidea by BRONWEN J. SCOTT & RON KENNY	694–702
Apogastropoda by WINSTON F. PONDER	703
Superorder Caenogastropoda by WINSTON F. PONDER	703
Superfamily Cyclophoroidea by JOHN STANISIC	703–706
Superfamily Ampullarioidea by JOHN STANISIC	706–707
Sorbeoconcha WINSTON F. PONDER	707
Superfamily Cerithioidea by JOHN M. HEALY & FRED E. WELLS	707–733
Superfamily Campaniloidea by JOHN M. HEALY & FRED E. WELLS	733–737
Infraorder Littorinimorpha by WINSTON F. PONDER	737
Superfamily Littorinoidea by DAVID G. REID	737
Family Littorinidae by DAVID G. REID	738–739
Family Pickworthiidae by PHILIPPE BOUCHET & J. LE RENARD	739–741
Superfamily Cingulopsoidea by WINSTON F. PONDER & ROGER G. DE KEYZER	741–744
Superfamily Rissooidea by WINSTON F. PONDER & ROGER G. DE KEYZER	745–766
Superfamily Stromboidea by FRED E. WELLS	766–769
Superfamily Vanikoroidea by WINSTON F. PONDER	769–772
Superfamily Calyptraeoida by K. ELAINE HOAGLAND & WINSTON F. PONDER	772–774
Superfamily Capuloidea by WINSTON F. PONDER	774–775
Superfamily Xenophoroidea by WINSTON F. PONDER & ROGER G. DE KEYZER	775–778
Superfamily Vermetoidea by FRED E. WELLS	778–780
Superfamily Cypraeoida by BARRY WILSON	780–786
Superfamily Velutinoidea by BARRY WILSON	786–790
Superfamily Naticoidea by ALAN R. KABAT	790–792
Superfamily Tonnoidea by ALAN G. BEU	792–803
Superfamily Carinarioidea by LESLIE NEWMAN	804–808
Infraorder Ptenoglossa by WINSTON F. PONDER	808
Superfamily Triphoroidea by FRED E. WELLS	808–811
Superfamily Janthinoidea by BRIAN J. SMITH	811–817
Superfamily Eulimoidea by BRIAN J. SMITH	817–818
Infraorder Neogastropoda WINSTON F. PONDER	819
Superfamily Muricoidea by WINSTON F. PONDER	819–820
Family Muricidae by WINSTON F. PONDER	820–824
Family Turbinellidae by M.G. HARASEWYCH	824–825
Family Buccinidae by M.G. HARASEWYCH	825–827
Family Columbelloidea by BARRY WILSON	827–829
Family Nassariidae by M.G. HARASEWYCH	829–831
Family Melongenidae by M.G. HARASEWYCH	831–832
Family Fasciolaridae by M.G. HARASEWYCH	832–833
Family Volutidae by THOMAS A. DARRAGH & WINSTON F. PONDER	833–835
Family Olividae by BRIAN J. SMITH	835–837
Family Harpidae by BRIAN J. SMITH	837–838

Family Marginellidae by WINSTON F. PONDER	838–841	Order Eupulmonata by JOHN STANISIC	1076
Family Mitridae by WINSTON F. PONDER	841–842	Superfamily Ellobioidea by JOHN STANISIC	1076–1078
Family Volutomitridae by WINSTON F. PONDER	842–843	Superfamily Trimusculoidea by JOHN STANISIC	1078–1079
Family Costellariidae by WINSTON F. PONDER	843–845	Suborder Stylommatophora by JOHN STANISIC	1079–1080
Superfamily Cancellarioidea by M.G. HARASEWYCH & RICHARD E. PETT	845–846	Infraorder Orthurethra by JOHN STANISIC	1080
Superfamily Conoidea by ALAN J. KOHN	846–854	Superfamily Achatinelloidea by JOHN STANISIC	1080–1081
Superorder Heterobranchia by WINSTON F. PONDER	854	Superfamily Cionelloidea by JOHN STANISIC	1081
Superfamily Valvatoidea by WINSTON F. PONDER & ROGER G. DE KEYZER	854–858	Family Cionellidae by BRIAN J. SMITH	1081–1082
Superfamily Architectonicoidea by JOHN M. HEALY	858–862	Superfamily Pupilloidea by JOHN STANISIC	1082
Superfamily Rissoelloidea by WINSTON F. PONDER & ROGER G. DE KEYZER	862–864	Family Pupillidae by JOHN STANISIC	1082–1084
Superfamily Omalogyroidea by WINSTON F. PONDER & ROGER G. DE KEYZER	864–865	Family Pleurodiscidae by BRIAN J. SMITH	1084
Superfamily Pyramidelloidea by WINSTON F. PONDER & ROGER G. DE KEYZER	865–869	Family Valloniidae by JOHN STANISIC	1084–1085
16 OPISTHOBRANCHIA	915–1035	Superfamily Partuloidea by JOHN STANISIC	1085–1086
Introduction by WILLIAM B. RUDMAN & RICHARD C. WILLAN	915–942	Infraorder Sigmurethra by JOHN STANISIC	1086
<i>History of Discovery, Morphology and Physiology,</i> <i>Natural History by William B. Rudman</i>		Superfamily Achatinoidea by JOHN STANISIC	1087
<i>Definition and General Description, Phylogeny, Biogeography,</i> <i>Methods of Study by Richard C. Willan</i>		Family Ferrussaciidae by BRIAN J. SMITH	1087
Order Cephalaspidia by ROBERT BURN & T.E. THOMPSON	943–959	Family Subulinidae by ALAN SOLEM	1087–1088
Order Acochlidea by ROBERT BURN	959–960	Family Megaspiridae by JOHN STANISIC	1088–1089
Order Rhodopemorpha by ROBERT BURN	960–961	Family Achatinidae by JOHN STANISIC	1089–1090
Order Sacoglossa by ROBERT BURN	961–974	Superfamily Streptaxoidea by JOHN STANISIC	1090–1091
Order Anaspidea by RICHARD C. WILLAN	974–977	Superfamily Rhytidoidea by JOHN STANISIC	1091
Order Notaspidea by RICHARD C. WILLAN	977–980	Family Rhytididae by BRIAN J. SMITH	1091–1093
Order Thecosomata by LESLIE NEWMAN	980–985	Superfamily Acavoidea by JOHN STANISIC	1093
Order Gymnosomata by LESLIE NEWMAN	985–989	Family Caryodidae by BRIAN J. SMITH & RON C. KERSHAW	1093
Order Nudibranchia by RICHARD C. WILLAN	990	Superfamily Bulimuloidea by JOHN STANISIC	1093–1094
Suborder Doridina by WILLIAM B. RUDMAN	990–1001	Family Bulimulidae by ALAN SOLEM	1094–1096
Suborder Dendronotina by WILLIAM B. RUDMAN	1001–1007	Superfamily Arionoidea by JOHN STANISIC	1096
Suborder Arminina by RICHARD C. WILLAN	1007–1011	Family Punctidae by JOHN STANISIC	1096–1097
Suborder Aeolidina by WILLIAM B. RUDMAN	1011–1017	Family Charopidae by JOHN STANISIC	1097–1099
17 PULMONATA	1037–1125	Family Helicodiscidae by ALAN SOLEM	1100
Introduction by BRIAN J. SMITH & JOHN STANISIC	1037–1061	Family Arionidae by BRIAN J. SMITH	1100–1101
<i>Definition and General Description, History of Discovery,</i> <i>Morphology and Physiology (External Features, Musculature</i> <i>and Locomotion, Feeding and Digestion, Circulation), Methods</i> <i>of Study by Brian J. Smith</i>		Superfamily Limacoidea by JOHN STANISIC	1101–1102
<i>Morphology and Physiology (Excretion, Respiration, Sense</i> <i>Organs and Nervous System, Reproduction, Embryology) Natural</i> <i>History, Economic Significance, Biogeography, Fossil Record by</i> <i>John Stanisic</i>		Family Limacidae by BRIAN J. SMITH	1102–1103
Order Systellommatophora by JOHN STANISIC	1060–1067	Family Milacidae by BRIAN J. SMITH	1103
Order Basommatophora by JOHN STANISIC	1067–1075	Family Zonitidae by BRIAN J. SMITH	1104
		Family Trochomorphidae by JOHN STANISIC	1104–1105
		Family Helicarionidae by BRIAN J. SMITH	1105–1106
		Family Cystopeltidae by BRIAN J. SMITH & RON C. KERSHAW	1106–1107
		Family Testacellidae by BRIAN J. SMITH	1107–1108
		Superfamily Succinoidea by JOHN STANISIC	1108
		Family Succineidae by ALAN SOLEM	1108–1109
		Family Athoracophoridae by JOHN STANISIC	1109–1110
		Superfamily Polygyroidea by JOHN STANISIC	1110–1112
		Superfamily Camaenoidea by JOHN STANISIC	1112
		Family Camaenidae by ALAN SOLEM	1112–1113
		Superfamily Helicoidea by JOHN STANISIC	1113
		Family Helicidae by BRIAN J. SMITH	1113–1114
		Family Bradybaenidae by JOHN STANISIC	1115

CLASS GASTROPODA

CHAPTER 14

DEFINITION AND GENERAL DESCRIPTION

More than half of all molluscan species are gastropods. Not only are gastropods speciose and numerous, they rank also among the most diverse of all animal groups and second only to the Insecta in terms of diversity as a class. Gastropods represent an extremely plastic group of organisms. They range from primitive marine species to highly evolved terrestrial air-breathing snails and slugs, and are found in almost all terrestrial, freshwater and marine habitats. Some indication of the morphological diversity within the class is shown in Plates 22–37. They may crawl, burrow, swim, float or be sedentary, and they include grazers on vegetation, carnivores and parasites. Estimates of the number of living species range from 105 800 (Jaekel 1958 in Boss 1971) to 67 000 (Solem 1974a) and 37 500 (Boss 1971). The numbers alone indicate an extraordinarily viable group.

The gastropod body consists of a head bearing a terminal mouth, tentacles and eyes, a visceral mass largely made up of gonad and digestive system, and a large foot with a creeping sole (Fig. 14.1). Characteristically the visceral mass is wound in a right-hand helicoid spiral and is enclosed in a shell secreted by its covering epithelium, the mantle. The shell encloses the mantle cavity. In many gastropods the head and foot can be withdrawn into the cavity which lies over the head. These features basically form two major functional regions. The upper part of visceral mass and mantle, the visceropallium, is involved with digestion, circulation, reproduction and excretion and functions largely through mucous and ciliary action. The lower part, the head-foot, is associated with the external environment, movement and feeding and is largely muscular, although it too is provided with cilia and mucous cells, and is involved in sensory perception.

Torsion and Asymmetry

Gastropods are unique among all animals in that they are consistently asymmetrical. In most, the anus and opening of the kidneys are anterior and discharge over the animal's head; the long nerve connectives are twisted and crossed into a figure-of-eight, and the intestine is twisted on itself and loops back into the visceral mass (Fig. 14.2B). This arrangement of organ systems occurs secondarily, during development, for the larval gastropod is bilaterally symmetrical. Its anus and kidney openings are situated posteriorly and about a third of the body consists of a dorsal hump containing the visceral mass, the mantle and the mantle cavity; this larval arrangement resembles that of the hypothetical pre-torsional ancestral mollusc (Figs 1.2, 14.2A). At some point in development, an embryological rotation occurs either as a result of the contraction of differentially developed larval retractor muscles (Smith 1935; Crofts 1937, 1955) or even before the muscles are developed. In schematic form, the head and foot remain fixed, but the dorsal hump rotates 180°. In the abalone genus, *Haliotis*, the process may take several days (Crofts 1937) and occurs in two stages. The rapid first stage is initiated by contraction of the velar retractor muscle; the slower second stage involves the differential growth of larval

structures. In opisthobranchs there is an additional stage; torsion may be complete within a few hours (Tardy 1991), and a countermovement, sometimes called detorsion, again places the mantle cavity and anus in a posterior position and the body becomes bilaterally symmetrical (Kandel 1979).

The functional significance of torsion has been the subject of much debate. Recent discussions include those of Ghiselin (1966a), Batten, Rollins & Gould (1967), Linsley (1978a, 1978b), Lever (1979), Pennington & Chia (1985), Haszprunar (1988a),

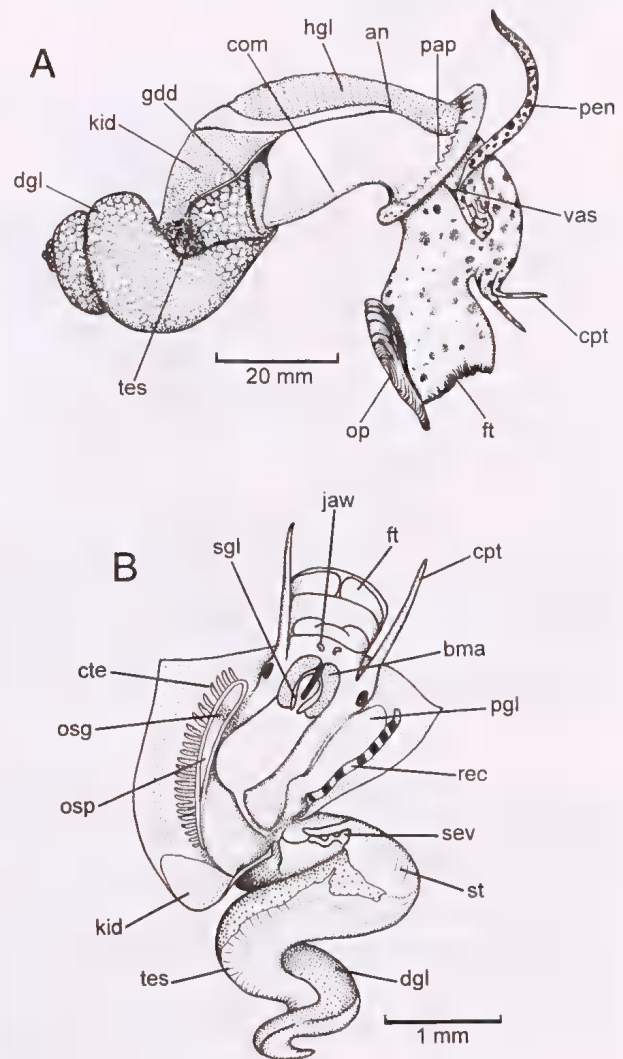


Figure 14.1 Gastropods removed from the shell to show the internal anatomy. A, *Cymatium nicobaricum* (Ranellidae), male, right view. B, *Eatoniella olivacea* (Eatoniellidae), dorsal view, with mantle opened out. an, position of anus; bma, buccal mass; com, columellar muscle; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; ft, foot; gdd, gonadal duct; hgl, hypobranchial gland; jaw, jaw; kid, kidney; op, operculum; osg, osphradial ganglion; osp, osphradium; pap, pallial papillae; pen, penis; pgl, prostate gland; rec, rectum; sev, seminal vesicle; sgl, salivary gland; st, stomach; tes, testis; vas, vas deferens. (A, after Houbbrick, J.R. & Fretter 1969; B, after Ponder 1968) [M. Thompson]

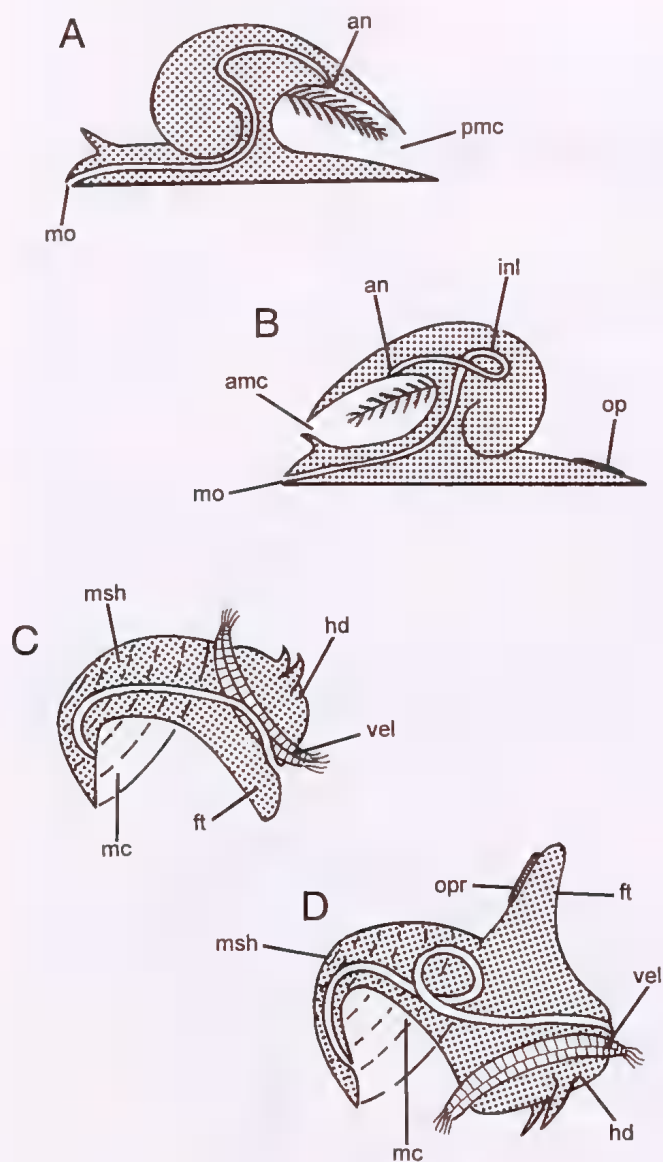


Figure 14.2 The shift in position of the mantle cavity and the intestine resulting from torsion, diagrammatic representation. A, an hypothetical pre-torsional ancestral gastropod. B, a primitive gastropod after torsion with anterior mantle cavity and twisted intestine. C, a veliger larva before torsion with head and velum the last parts to be retracted into the shell. D, a post-torsional veliger larva with the foot retracted into the shell last. amc, anterior mantle cavity; an, anus; ft, foot; hd, head; inl, internal organs looped; mc, mantle cavity; mo, mouth; msh, mantle shell; opr, operculum rudiment; pmc, posterior mantle cavity; vel, velum. (After Russell-Hunter 1979) [M. Thompson]

Edlinger (1988) and Voltzow (1987). Garstang (1929) suggested that the immediate advantage of torsion is to the larva when the mantle cavity is brought over the head, as the larva can then retract the velum into the mantle cavity (Fig. 14.2C, D). However, an experiment with pre-torsional and torsional larvae demonstrated that, except in one instance, no predator species ate significantly fewer torted than pre-torsional veligers (Pennington & Chia 1985). In adults, as a result of torsion, the shell can be effectively clamped over the head region and circulation patterns in the mantle cavity are improved (Yonge 1947; Linsley 1978a).

Traditionally, torsion has been treated as an issue separate from that of the asymmetrical coiling of the gastropod shell. However, marked asymmetries remain in internal anatomy even in those gastropods in which the shell is lost and there has been a secondary return to bilateral symmetry of external features. Solem (1974a) argued that tilting of the asymmetrical shell may have provided the initial impetus for torsion. Runnegar (1981) suggested that torsion and asymmetry are intimately related in the

phylogenetic sense in that asymmetric shells would be difficult to balance unless the shell and the viscera it contains are moved to a more suitable position, as happens in detorsion.

Most turbanate-shelled gastropods are dextrally coiled, and there is a consequent reduction of the pallial organs of the right side so that only the left ctenidium persists (Fig. 14.16B). Similarly the internal organs are reduced and in the 'higher' gastropods there remain only the left auricle of the heart (monotocardia), the left kidney and a single gonad opening to the exterior via what was originally the right urinogenital coelomoduct.

CLASSIFICATION

The first gastropod classifications were based on the shape of the shell. Later, when organ systems were investigated, major groupings were erected on the basis of the arrangement of the gills, the heart, and the position of the mantle cavity. It is from these classifications that terms such as Monotocardia and Dibranchia, often seen in textbooks, were devised. However, the biggest impact on gastropod classification came from the investigation of the nervous system (Spengel 1881; Bouvier 1887) and the radula (Troschel 1856–1893). These works resulted in sophisticated classifications that were in large part in accord. Space does not permit a detailed summary of the complex and fascinating early history of gastropod classification, but Cox (1960b) provided an excellent account.

The most influential modern classification of gastropods was that of Thiele (1929–1931). He integrated the earlier classifications based primarily on separate organ systems, although he emphasised the importance of the radula, respiratory and nervous systems. He recognised as subclasses the Prosobranchia, Opisthobranchia and Pulmonata. The Prosobranchia were divided into three orders, Archaeogastropoda, Mesogastropoda and Neogastropoda, each representing a higher level of advancement. This classification was adopted enthusiastically by nearly all molluscan workers, including the authors of major monographic treatments (for example, Wenz 1940; Hyman 1967; Boss 1982). The Pulmonata and Opisthobranchia were lumped into a single group Euthyneura by some (Boettger 1954; Zilch 1959–1960; Taylor & Sohl 1962; Salvini-Plawen 1990), following Spengel (1881), but this was not commonly adopted. This classification was so entrenched that it was not until the latter half of the 1980s that it was substantially modified. Indeed the chapters commissioned for this work were based on this classification, which is why the main summary descriptive sections are arranged under Thiele's system.

However, by the 1960s flaws were noticed in the otherwise apparently impregnable Thiele classification. Investigation of some small, enigmatic gastropods showed strange anatomies that could not easily be explained away entirely by invoking 'modification due to small size'. The catchall baskets such as the Rissooidea (= Truncatelloidea) in which all small gastropods with simple shells were placed, proved to very heterogeneous assemblages. Two such groups (Rissoellidae and Omalogyridae) were investigated by Fretter as early as 1948, who later (Fretter & Graham 1960) admitted their similarity to opisthobranchs. Pyramidellids, long classified with mesogastropods, were shown to be opisthobranchs by Fretter & Graham (1949), although their shells had caused them to be placed near the totally unrelated Eulimidae. Kosuge (1966) investigated the Triphoridae and concluded that they had characters that were neither prosobranch or opisthobranch; he created the new group Heterogastropoda for these and several other families, most of which are now known to be completely unrelated. Additional anomalous groups, the Architectonicoidea and Epitoniidae, were investigated by Robertson (1985) who (incorrectly) concluded they are related to one another. The step-like nature of Thiele's classification of prosobranchs was questioned when Ponder (1973) reassessed the relationships of the Neogastropoda and concluded that this group was not derived from highly advanced mesogastropods as had been thought previously.

Table 14.1 A comparison of the gastropod classification used in this work, and the 'traditional' classification.
*Probably paraphyletic (see Ponder & Lindberg 1996).

This work	'Traditional' classification
Class Gastropoda	Class Gastropoda
	Subclass Prosobranchia
Subclass Eogastropoda (including Patellogastropoda)	Order Archaeogastropoda
Subclass Orthogastropoda	
Superorder Cocculiniformia *	Order Archaeogastropoda
Superorder Neritopsina	Order Archaeogastropoda
Superorder Vetigastropoda	Order Archaeogastropoda
Superorder Caenogastropoda	
Order Architaenioglossa	Order Mesogastropoda
Order Sorbeoconcha	
Infraorder Littorinimorpha	Order Mesogastropoda
Infraorder Ptenoglossa	Order Mesogastropoda
Infraorder Neogastropoda	Order Neogastropoda
Superorder Heterobranchia	
Order Opisthobranchia	Subclass Opisthobranchia
Order Pulmonata	Subclass Pulmonata

Some Russian workers also produced variant classifications, usually involving the creation of a great number of additional higher taxa. The most often cited (because it is published in English) is that of Golikov & Starobogatov (1975). Although these classifications have generally not been adopted by western scientists, Golikov & Starobogatov (1975) made a major advance in recognising the patellid limpets as being the most primitive living gastropods. This concept was at variance with earlier gastropod classifications in which species such as pleurotomariids with a coiled shell bearing a slit were seen as the most primitive gastropods (for example, Fretter & Graham 1962; Morton & Yonge 1964; Graham 1985). Recent classifications and thinking have reinforced the idea of the patellid limpets being a very primitive group which is quite distinct from other gastropods (Wingstrand 1985; Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a; Lindberg 1988; Salvini-Plawen 1988). The recognition of the distinctive nature of the true limpets was formalised by Lindberg (1988), who coined the name Patellogastropoda for them. Salvini-Plawen (1980) had already coined the term Vetigastropoda for the major part of the old Archaeogastropoda, minus several groups, principally the Neritoidea and Patellogastropoda. The characters defining this grouping have been discussed in detail by Salvini-Plawen & Haszprunar (1987).

The recent use of transmission electron microscopy to study sperm (Healy 1988 and references therein) and osphradia (Haszprunar 1985a, 1985b) provided a wealth of new data which led to a major reassessment of the higher classification of gastropods in the late 1980s (Haszprunar 1985c, 1988a, 1988b; Salvini-Plawen & Haszprunar 1987; Ponder & Warén 1988). Coupled with these findings was the discovery of a wealth of new organisms that seemed to bridge gaps or were entirely new groups, many of these being found in the deep sea associated with hydrothermal vents (Fretter, Graham & McLean 1981; McLean 1981, 1988a, 1988b, 1989a, 1989b, 1990a, 1990b; Fretter 1988, 1989, 1990; Haszprunar 1989a, 1989b; Warén & Bouchet 1989; Warén & Ponder 1991). The relict Australian gastropod genus *Campanile* was investigated by Houbbrick (1981a, 1989) and

shown to have several very unusual features which were regarded as intermediate between those of the 'prosobranchs' and opisthobranchs by Haszprunar (1985c, 1988a, 1988b), although this was disputed by Healy (1986), Ponder & Warén (1988) and Houbbrick (1989) who regarded *Campanile* as a caenogastropod.

Haszprunar (1988a), in his seminal paper on gastropod classification, reassessed all of this new information and provided the basis for a new classification of gastropods. Some aspects of his methodology have been criticised by Bieler (1990) and replied to by Haszprunar (1990). Most aspects of this classification are followed by Ponder & Warén (1988), with some modifications, in their classification of the Caenogastropoda and lower Heterobranchia. Gastropod classification was reviewed recently by Bieler (1992) and Ponder & Lindberg (1996, 1997), and is discussed in more detail in the next chapter.

The main changes made to Thiele's classification by Haszprunar are:

1. The Archaeogastropoda is a paraphyletic group. Salvini-Plawen (1980) coined the name Vetigastropoda for the majority of the familiar animals called Archaeogastropoda and this unambiguous term is preferred, although Hickman (1988) has argued for the continued use of Archaeogastropoda in a restricted (= Vetigastropoda) sense. The Neritopsina, Patellogastropoda, Cocculiniformia and Vetigastropoda are of equal rank.
2. The Caenogastropoda, a grouping proposed by Cox (1960a), comprises the Mesogastropoda and Neogastropoda. Haszprunar (1988a) excluded the Architaenioglossa (Cyclophoroidea + Ampullarioidea) but these are included by Ponder & Warén (1988) and this is the arrangement followed here, although the monophyly of the Architaenioglossa is uncertain.
3. Following Haszprunar (1985b) the name Heterobranchia is used for a grouping containing the Opisthobranchia and Pulmonata (= Euthyneura) together with a paraphyletic group called 'Allogastropoda' by Haszprunar (1985b, 1988a), Triganglionata by Haszprunar (1985c) and Heterostropha (Ponder & Warén 1988).

14. CLASS GASTROPODA

At present the higher classification of gastropods is still largely in a state of flux. For example, Salvini-Plawen (1990) formally recognised two subclasses – Streptoneura and Euthyneura [equivalent to the Prosobranchia and Euthyneura (= Opisthobranchia and Pulmonata)], but in so doing the prosobranchs (Streptoneura) are paraphyletic.

The Patellogastropoda is now considered to be the most primitive gastropod group; its members differ from other gastropods very significantly. This group, probably more so than any other, deserves subclass status (see Patellogastropoda for summary of distinctive features). Despite the currently unsettled nature of gastropod phylogeny and classification, an approach has been adopted in this work that reflects the status of what appear to be the main monophyletic groups. One major new change is the introduction of a new subclass name, Orthogastropoda, for all gastropods other than the Patellogastropoda and their presumed coiled ancestors. For this latter group the name Eogastropoda has been coined. Within Orthogastropoda several superorders are recognised (see below), but the traditional subclasses are not maintained, thus avoiding the problems of paraphyly.

The classification adopted here is a compromise between the changes made in recent literature and the 'traditional' classification (see Table 14.1). It largely follows Haszprunar's (1988a) classification, but is modified according to the findings of a more recent analysis of gastropod phylogeny by Ponder & Lindberg (1996). This approach is taken partly because the text was originally designed around the Prosobranch–Opisthobranch–Pulmonate trichotomy and chapters were written for these as subclasses. These chapters have been maintained as reviews of the groups that they represent, even though the names Pulmonata and Opisthobranchia are no longer maintained as subclasses. A modern classification is provided with a brief introduction to each higher grouping.

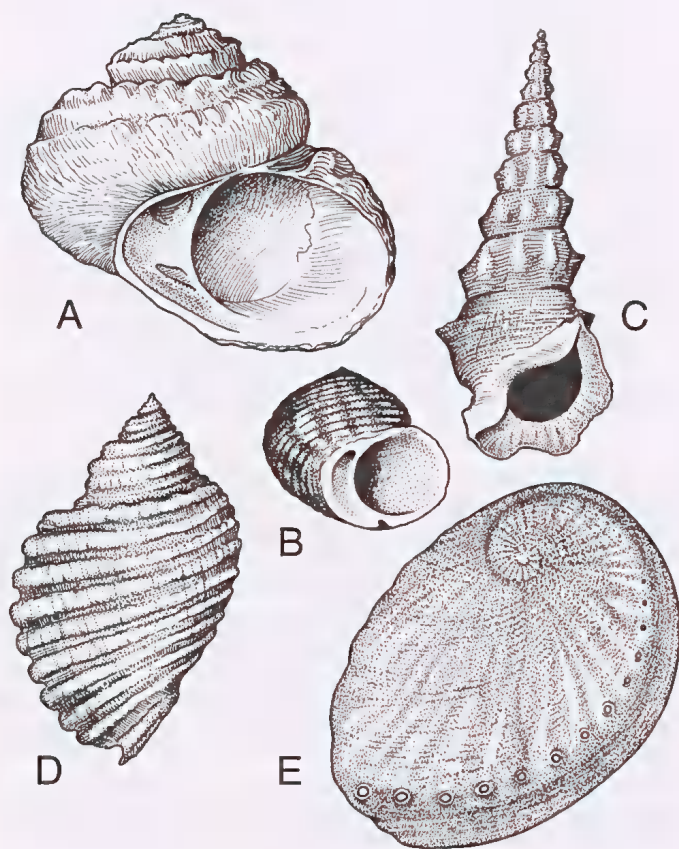


Figure 14.3 Shells collected in Botany Bay, New South Wales, by naturalists on the Cook expedition in 1770. A, *Turbo torquatus* (Turbinidae). B, *Subnirrella undulata* (Turbinidae). C, *Pyrazus ebeninus* (Potamididae). D, *Dicathais orbita* (Muricidae). E, *Haliotis ruber* (Haliotidae). (After Whitley 1970) [M. Thompson]

HISTORY OF DISCOVERY

As might be expected, the history of studies on Australian Gastropoda has been decidedly uneven. The molluscan fauna of this large continent was almost unknown until relatively recently, and the rate and direction of studies on gastropods have varied markedly, often as a result of the interest of one or a few individuals. Among these fluctuations have been changes in the rate of the documentation of the fauna over time, different rates of investigation of various habitats and uneven progress in the examination of major taxonomic groups.

Early Exploration

The first illustrations of Australian gastropods were those of shells collected by naturalists of the Cook expedition in Botany Bay, New South Wales in 1770 (Fig. 14.3). Studies on the gastropods of Australia thus began with the early European exploratory voyages to the continent. Much of this early work was done by the French. One of the early voyages was that of the Baudin expedition (1801–1804) with the ships *Le Géographé* and *Le Naturaliste*. A considerable number of specimens collected during that voyage were taken to Europe where they were described by such eminent malacologists as Lamarck, Montfort, Blainville, Kiener and Chenu. Molluscs collected during the four surveys of the northern Australian coast by Lieutenant Phillip King (1818–1822) were described by J.E. Gray (King 1927). At about the same time, the French ships *Uranie* and *Physicienne* visited Australia. Molluscs collected on this voyage were described in conjunction with those from the third and probably the most important of these early French voyages in the present context – that of the *l'Astrolabe* (1826–1829), under Admiral Dumont D'Urville (Quoy & Gaimard 1830–1834).

Subsequently, collections made by Preiss in Western Australia were described by Menke (1843). After this early period, when a great number of species were described from Australia, the rate of discovery slowed. Smith reported on some of the shells collected by J.J. Walker during a surveying cruise of the *Penguin* in 1890–1891. In the early 1900s the German *Meteor* expedition visited Western Australia. The molluscan material collected was discussed by Thiele (1930) as part of a series of volumes on the expedition; Ponder (1978) recently illustrated Thiele's previously unfigured type specimens.

A more complete account of the early exploratory voyages is given in Chapter 1.

Amateurs and Curators

In the latter half of the nineteenth century the collecting emphasis changed from exploratory voyages to individual activities, mainly by keenly interested amateurs (see also Chapter 1). Names such as George French Angas, John (William) Brazier, Sir Joseph Verco, Edwin Ashby, Charles John Gabriel, John Henry Gatliff, Hereward Kesteven, William Lewis May and William George Torr dominate the molluscan literature of Australia of the late nineteenth and early twentieth centuries.

All were amateurs, except Angas, who worked at the Australian Museum for several years. The amateurs developed their own private collections and libraries, most of which eventually went to public museums where they form the core of the collections. The work of these 'amateurs' was often extensive. For example, Gatliff and Gabriel dominated Victorian malacology for three-quarters of a century (Smith & Black 1969). Between them, often in co-authorship, Gatliff and Gabriel published 84 papers in which were described five new genera and 149 new species.

Museums in Australia began to appoint salaried staff to curate their mollusc collections in the early 1900s. The early curators lacked formal academic qualifications but more than compensated by their tremendous contribution to the scientific literature. Foremost among the early curators was Charles Hedley, who retired as curator of conchology in 1924 at the Australian Museum after

33 years. Iredale (1956) listed 236 scientific papers by Hedley covering a wide range of topics. Iredale himself had a long tenure at the Australian Museum. He wrote more than 170 papers on molluscs and proposed more than 2000 scientific names (Whitley & Ponder 1973). Regrettably Iredale was an excessive 'splitter' and the value of his work is diminished by the extensive number of taxa which have been synonymised subsequently. Joyce Allan, also of the Australian Museum, was another active writer, and contributed 113 articles and papers on molluscs and two books, on Australian shells and cowries (Allan 1950, 1958; see Whitley 1968). Bernard Charles Cotton published 185 papers and books, primarily on molluscs, during the forty years he worked at the South Australian Museum (Laws & Mincham 1968).

Checklists and Monographs

The early mollusc work dealt primarily with faunistic studies, and the extensive literature appeared over the decades in many journals and other sources. Perhaps the most important publications of earlier malacologists were the papers and books drawing together the available information in the form of monographs and checklists. While these early checklists contain errors and misidentifications, they have considerable value in providing modern workers with an easy entry into older literature.

No attempt has been made to draw together a complete listing of the gastropod fauna, although a series of state lists has been prepared. Angas (1867a, 1867b) was the first to produce a list, that of the marine molluscs of Port Jackson Harbour, New South Wales. His initial list consisted of some 450 species. A few additional records were added the following year by Cox (1868) in a privately published list. Angas (1871, 1877) added considerably to the list to raise the total number of species to about 750. Hedley (1918) expanded the check-list further to 1200 species, and enlarged it to cover the marine molluscs from all of New South Wales. The most recent list of the marine molluscs of New South Wales is that of Iredale & McMichael (1962), which records over 2000 species.

In Victoria, Pritchard and Gatliff published the *Catalogue of the Marine Shells of Victoria* in a series of nine parts in the Proceedings of the Royal Society of Victoria between 1898 and 1906. This was revised subsequently by Gabriel (1936) and Macpherson & Gabriel (1962). May's first Tasmanian list, published in 1923, was revised by Macpherson (May & Macpherson 1958). A series of 15 papers by Cotton & Godfrey on South Australian shells in the South Australian Naturalist between 1931 and 1935 became the basis for books on South Australian bivalves (Cotton 1938), and the remaining molluscan groups other than gastropods (Cotton & Godfrey 1940). However, with the exception of archaeogastropods, gastropods were neglected, even when Cotton (1959, 1961, 1964) updated the work later with books on chitons and bivalves. Ripplingale & McMichael (1961), and more recently, Short & Potter (1987) produced popular books on Queensland molluscs.

Hedley (1915) produced the only checklist of Western Australian molluscs. Cotton was working on a book on the marine molluscs of Western Australia at the time of his death, but it was never published. The book by Wilson & Gillett (1979) contains considerable information on the 'prosobranchs' of Western Australia. More recent work by Wells & Bryce (1986) deals with the large-sized 'prosobranchs' and opisthobranchs, Rudman (1984, 1986a, 1987a, 1988) and Rudman & Avern (1989) reviewed many of the dorid opisthobranchs, and Wilson (1993, 1994) summarised the gastropods.

Non-marine Molluscs

Our knowledge of non-marine molluscs has proceeded less rapidly than has work on marine molluscs; the Victorian, New South Wales and Queensland mollusc lists discussed above are restricted to marine species. A checklist of the South Australian gastropods, including the freshwater and terrestrial species, was prepared by Cotton & Godfrey (1939). Iredale (1937a, 1937b, 1938, 1943) published lists of the land and freshwater molluscs of

Australia. The list of terrestrial molluscs was updated at the generic level by Burch (1978). More recently Smith & Kershaw (1979, 1981) have produced volumes on the non-marine molluscs of south-eastern Australia and Tasmania, and the Australian non-marine molluscs were catalogued by Smith in 1992.

The extensive monographic series by Solem (1979, 1981a, 1981b, 1984, 1985, 1988) examined the land snails of the large family Camaenidae, primarily in the Kimberley region of Western Australia and in the centre of the continent. Stanisic (1987, 1990) studied the systematics and biogeography of the extensive radiation of the Charopidae in tropical and subtropical Australia. Several components of the endemic radiation of hydrobiid snails have been described, including the faunas of artesian springs (Ponder, Hershler & Jenkins 1989; Ponder & Clark 1990), Queensland rainforest (Ponder 1991) and freshwater habitats of Tasmania and southern Victoria (Ponder 1992; Ponder, Clark, Miller & Toluzzi 1993; Ponder, Colgan, Clark, Miller & Terzis 1994).

Marine Molluscs

The larger marine species, at least those in shallow water, are fairly well known and a number of monographic treatments of individual families and genera have been published (details under individual families). Smaller species are poorly known. For example, the works of Laseron (1951, 1957, 1959) are important in this regard, as are the more recent studies by Ponder & Yoo (1976, 1980) and Ponder (1983a, 1984, 1985). The Opisthobranchia, a marine group, is poorly known and the available literature is scattered. The book by Willan & Coleman (1984) provided an overview of our knowledge of nudibranchs but appeared too soon to include all of the papers by Rudman (1982, 1983, 1984, 1985, 1986a, 1986b, 1986c, 1987b, 1988) on chromodorids.

THE GASTROPOD SHELL

Form and Structure

The gastropod shell is generally composed of an outer organic layer, the periostracum, and inner calcified layers primarily of calcium carbonate embedded in an organic matrix. Recent reviews of shell structure include those of Wilbur & Saleuddin (1983) and Watabe (1988). The shell covers and supports the visceral mass, and provides a cavity into which the head-foot can be retracted. Gastropod shells range in size from less than 1 mm in greatest dimension to more than 600 mm in length (*Syrinx aruanus* of Australian waters). The spectrum of gastropod shell shapes (Fig. 14.4) extends from slender, high-spined cones, such as those of the Turritellidae (Fig. 14.4E), to low-spined cap-shaped shells of limpets like *Cellana* (Fig. 14.4A), and includes shells with disjunct whorls (Fig. 14.4H). The external surface may be smooth and polished or elaborately sculptured. Recent workers (Raup 1961, 1966; Vermeij 1971a, 1971b, 1977, 1978a, 1978b, 1979; Linsley 1977, 1978a, 1978b; Signor 1983; Signor & Kat 1984) have proposed geometric descriptors of shell shape and speculated on the adaptive nature of form and function.

The shell lies outside the tissues and is secreted by histochemically differentiated regions of outer mantle epithelium and underlying calcium gland cells. An uncalcified, proteinaceous outer layer, the periostracum, is usually present. Its thickness varies with habitat, and it is especially noticeable in some gastropods that live in fresh water. Beneath the periostracum lie several layers of crystalline calcium carbonate in a matrix of glycoprotein (Fig. 1.12; Currey & Taylor 1974; Weiner & Hood 1975). The calcium carbonate is in the crystallographic form of calcite or aragonite; calcite and aragonite predominate in the shells of prosobranchs and stylommatophoran pulmonates, respectively.

Typically the outer region or ostracum forms the prismatic layer (Fig. 1.12A), comprising stacks of crystals lying perpendicular to the shell surface. Beneath the outer region in archaeogastropods is a middle layer of mother of pearl or nacre. Nacre consists of

blocks of aragonite arranged in sheets about 0.5 to 1 μm thick, separated by a thin layer of protein (Fig. 1.12B, C). Families and genera of limpets are distinguished on the basis of the microscopic structure of the nacre (Lindberg & Hickman 1986; Lindberg 1988). The major shell layer in most other gastropods is the crossed-lamellar layer (Fig. 1.12B). This layer is built up of large lamellae, each almost rectangular with the longer axis orientated horizontally or parallel to the shell surface. The shorter axes are mostly in a vertical position. These lamellae are formed of numerous smaller lamellae which in turn consist of smaller crystals. Variations in structure have both adaptive and taxonomic implications (MacClintock 1967; Vermeij 1978b; Lindberg & Hickman 1986). Families and genera of limpets, for example, are distinguished on the basis of shell structure (Lindberg & Hickman 1986; Lindberg 1988).

Shell Shape

Most gastropods have a single turbinate or helicoid shell. Successive whorls are laid down, one below the other, around a central axis, the columella. The fundamental characteristic of the coiled shell is such that '... the curve traced in space is, in all cases, an equiangular (logarithmic) spiral ...', as growth proceeds (Thompson 1942 in Raup 1961). The striking implication of a logarithmic spiral is that a snail shell does not change its shape as it grows, and is, therefore one of those '... certain things which suffer no alteration except in magnitude when they grow' (Aristotle, quoted by Illert 1983). Illert (1981, 1983, 1989) incorporated diurnal and long-term growth cycles, discontinuous shell growth, collateral growth lines and other features of shells in

a series of mathematical equations describing a general theory of spiral shell form. These elegant theoretical descriptions of shell shape and its implications were based on studies of the South Australian muricid *Pterynotus triformis*, amongst others.

Earlier work (Raup 1961, 1966) utilised four parameters in the quantitative description of a gastropod shell: the shape of the generating curve (S), its rate of expansion (W) during the production of one complete whorl, (D) the position of the generating curve relative to the axis of coiling, and the rate of whorl translation (T). Increasing rates of translation produce the relatively high-spined coiling types most common in gastropods (Figs 14.4D, E, 14.12). Planispiral shells are those in which the rate of expansion of the generating curve is low and the curve sufficiently far from the axis to produce an umbilicus (Fig. 14.4F, G). The generating curve of the abalone shell (Fig. 14.4B) lies nearly at right angles to the plane of the axis of coiling. The shells of gastropods are not randomly distributed across the total spectrum of possible forms (Fig. 14.5; Raup 1966). In a volume having dimensions W, T and D, most gastropods have shells for which W ranges mainly from near 1 to 10, T from 0 to 4 and D from 0 to 0.5 (Kohn & Riggs 1975).

The adaptive features of gastropod shell geometry include properties of the spiral and whorl overlap. Vermeij (1971b) described the relationship between angle of inclination and of the coiling axis, and associated them with the adaptive diversity of shell form in 'prosobranchs'. Small angles of inclination characteristic of siphonate gastropods are related to a diversity of shell shape greater than that possible among primitive forms with wide angles. The functional significance of high spired shells remains unclear, although it has been noted that shells of this type are usually restricted to burrowing species (Graus 1974) and that increasing spire height is correlated with reduced calappid crab predation in 'prosobranchs' (Vermeij 1977, 1978b).

In land snails, shell shape can be represented by a two dimensional graph of height on breadth (Cain 1978). In this representation most species occupy one or two modal areas: they are either high-spined or globular to disc-shaped. Very few occupy the intermediate space. The relationship between height and diameter of shells in free-crawling, fully retractile gastropods shows distinct patterns characteristic of major taxonomic groups (Cain 1978). In fully terrestrial stylommatophorans the distribution of height versus diameter is bimodal, even in faunas that are unrelated taxonomically, except for certain subfamilies in wet tropical regions. Terrestrial caenogastropods appear to take on characteristics of stylommatophorans when co-existing with them (Cain 1978).

The Aperture

The aperture is the outermost of the contiguous growth rings deposited in succession outwardly from the apical protoconch. It has been suggested that more functions are associated with this opening than any other single feature of the shell (Linsley 1978b); it is the exit through which the head-foot projects when the animal contacts the substratum, it receives the animal when the latter withdraws, and the current of water that flows through the mantle cavity passes in and out of the aperture.

The concepts of 'radial' and 'tangential' apertures were introduced by Linsley (1977) as criteria for inferring something about a gastropod's way of life. Gastropods that move actively clamp the shell to the substratum. To be effective in this position, the plane of the aperture must be tangential to the ventral portion of the body wall. This is the geometric shape seen in most living snails. The anterior portion of the tangential aperture may be elongated into a long, closed or open tube, through which the siphon is extended in caenogastropods such as *Cymatium muricatum*. Elaboration of the aperture by obstructions, elongation, and the development of folds, ridges, calluses and tubercles appear to be antipredator devices in gastropods both in marine environments (Vermeij 1975; Zipser & Vermeij 1978) and on land. In non-operculate land snails,

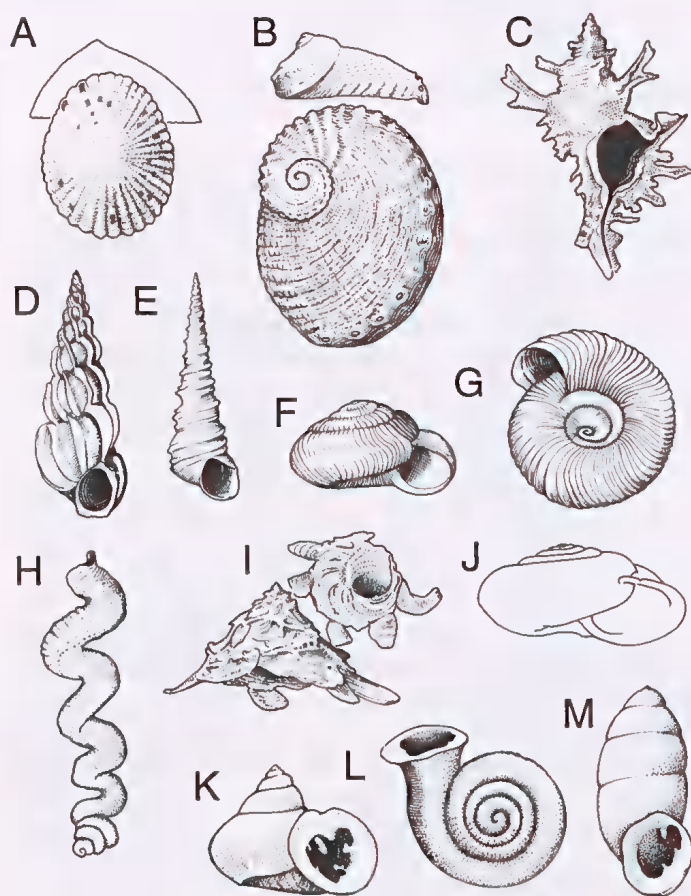


Figure 14.4 Some of the variation in form among gastropod shells. A, a limpet, *Cellana tramoserica* (Nacellidae). B, an abalone, *Haliotis cyclobates* (Haliotidae). C, *Chicoreus damicornis* (Muricidae). D, *Epitonium* sp. (Epitoniidae). E, *Stiracolpus atkinsoni* (Turritellidae). F, G, *Charopa albanensis* (Charopidae). H, *Tenagodus australis* (Siliquariidae). I, the carrier shell, *Xenophora peroniana* (Xenophoridae). J, *Torresitrachia torresiana* (Camaenidae). K, L, *Gylotrachela ningbingia* (Pupillidae), apertural and ventral view. M, a land snail, *Gastrocopta margaritae* (Pupillidae). (A-E, H, I, after Macpherson & Gabriel 1962; F, G, after Hedley 1892; K, L, after Solem 1981c; M, after Solem 1986) [M. Thompson]

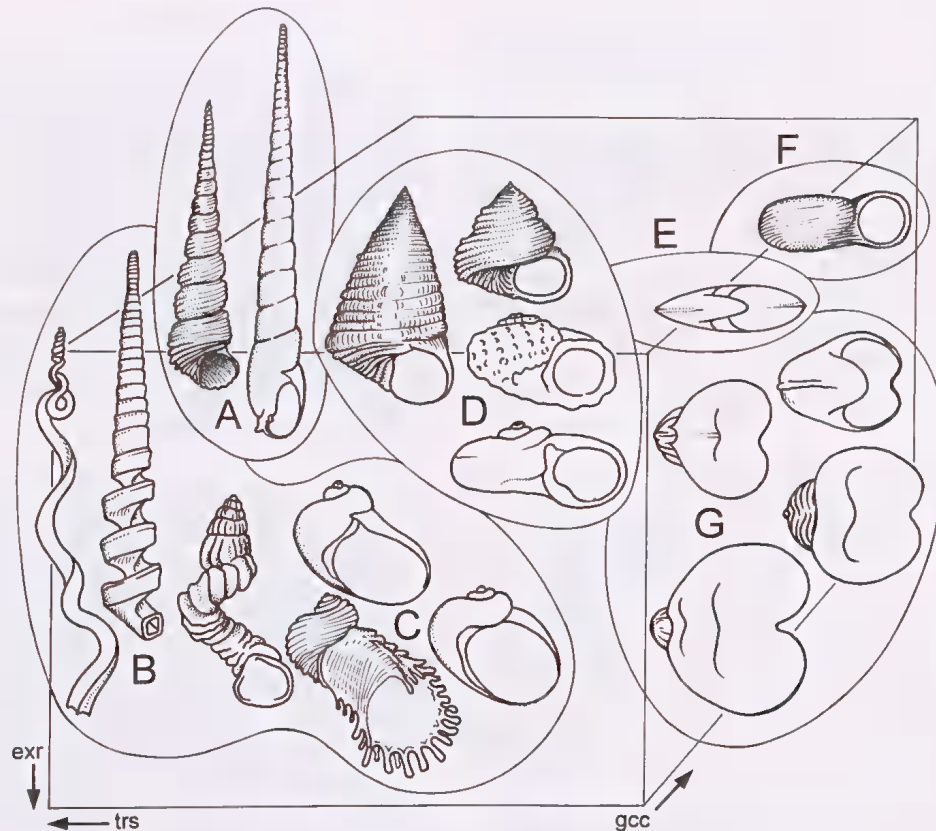


Figure 14.5 Gastropod shell shape in terms of coiling parameters within Raup's theoretical morphospace. A, high-spired gastropods with high translation and low expansion. B, high-spired shells with coiling open and irregular. C, low-spired shells with rapidly expanding generating curves. D, umbilicate and non-umbilicate trochiform shells. E, F, G, planispiral shells with low expansion rate. exr, direction of increasing expansion rate; gcc, direction of increasing distance of the generating curve from the axis of coiling; trs, direction of increasing translation. (After Hickman 1985b) [M. Thompson]

the development of folds, ridges, calluses, and tubercles (Fig. 14.4K, M) effectively narrows the shell aperture and appears to reduce predation by arthropods (Solem 1972b). Additionally, mucous plugs formed in the aperture of non-operculate land snails reduce water loss and may be so complex as to form an epiphragm or pseudo-operculum (Solem 1974).

The lip of the aperture serves as the generating curve, and corresponds to successive margins or lips of the shell which leave their impress as the shell grows. In many gastropods the impressions are very prominent, for example, the lamellae that ridge each whorl in some epitoniids (Fig. 14.4D) and the longitudinally arranged spines in some muricids (Fig. 14.4C). The spiny apertural lip in the Australian muricid *Pterynotus triformis* also functions as a vice when bivalves are pried open (Illert 1981), and the spiny apertural remnants of the Caribbean muricid *Ceratosoma foliatum* act as a hydrofoil during free fall (Palmer 1977).

Slits, notches, tremata and tubes are associated with ventilating the mantle cavity (Hickman 1985b) and may also be related to the aperture. In *Pleurotomaria* species the slit which excavates the outer lip of the aperture is functionally the site of elimination of the paired convergent exhalant streams of water flowing through the mantle cavity (Hickman 1985b), and indeed, most ventilating structures are involved with directing the flow of water in and out of the shell. However, the tremata of abalone (Fig. 14.4B) and the apical keyhole of fissurellids are quite separate from the aperture.

Features of the External Shell

Quite apart from shell shape, gastropod shells may be modified by two additional suites of external characters: shell sculpture *per se* and the incorporation of foreign material.

Shell sculpture is highly adaptive, and functions both as an antipredator device and as a means of facilitating burrowing in sediment. Patterns in gastropod shell architecture relative to predation have both a geographic and phylogenetic basis

(Vermeij 1978b). Vermeij (1988) reviewed other features of gastropod shell armour, including shell size and thickness, the limpet form, coiled form and retractability, and the compact shell and apertural barriers. A thick shell and sculpture reduce vulnerability to crushing by crabs (Vermeij 1975; Zipser & Vermeij 1978) and fish (Palmer 1979); the tenacity of the limpet foot discourages dislodgment and the low profile of the shell prevents apical breakage; shell coiling enables the foot and other soft parts to be withdrawn, and apertural barriers restrict entry.

In tropical waters, the high frequency of occurrence of a sculpture of stout spines correlates with the increasing intensity of shell crushing by fish, implying that fish predation has influenced the geographic distribution of sculptural type (Palmer 1979). In a study of burrowing gastropods from Guam and Pacific Panama, Vermeij & Zipser (1986) and Dudley & Vermeij (1989) found that rapid burrowing was associated with a smooth external shell surface and a large foot, whereas slow burrowers tended to have a small aperture and well-developed shell sculpture. Shell sculpture in high spired gastropods can facilitate burrowing in sediment (Signor 1983). Asymmetric ridges and tubercles function as ratchets, and prevent the shell from slipping backward when the animal extends its foot, but allow forward movement of the shell when the columellar muscle contracts. Kohn (1986) postulated that the sculpture of backward pointing tubercles in the cerithioidean genus, *Argyropeza*, functions in a similar manner.

The accretion of foreign material on the shell is widespread among gastropods. The shells of the cerithioidean genus *Scaliola* and some species of the vermetid genus *Serpulorbis* are encrusted with sand-sized grains. Material of various sizes is used in *Xenophora* species (Linsley & Yochelson 1973; Ponder 1983b), in which the dorsal surface of the shell is typically decorated with the shells of other gastropods, bivalves and scaphopods, and/or with gravel and pebbles (Fig. 14.4I). The shells of the sagdid land snails, *Thysanophora* species, are encrusted with soil and faecal matter glued together with mucus (Linsley & Yochelson 1973).

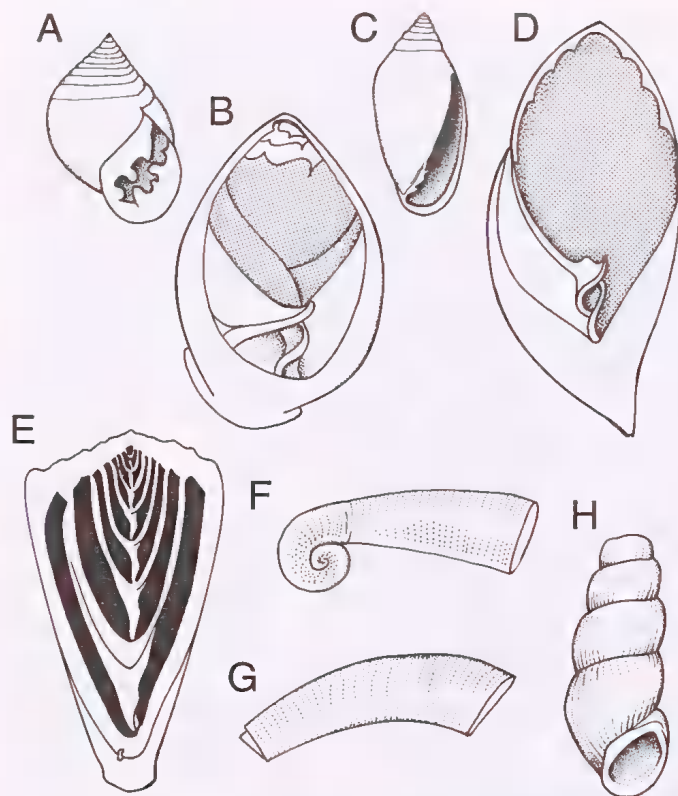


Figure 14.6 Shell modifications. A, B, shell resorption with loss of the columellar pillar in *Pythia* (Ellobiidae). C, D, shell resorption with loss of the columella and internal partitions in *Ellobium* (Ellobiidae). E, resorption of early whorls results in a greater volume in *Conus* (Conidae). F, G, the protoconch in *Caecum variegatum* (Caecidae) is cast off. H, decollate apical whorls in *Truncatella scalarina* (Truncatellidae). (A–D, after Morton 1955b; E, after Hickman 1985b; F, G, after Hughes 1985; H, after Smith & Kershaw 1979) [M. Thompson]

The Modified Shell

Shells once formed are not immutable (Fig. 14.6). They can be modified at the growing edge of the shell (Vermeij 1970), parts of the shell can be re-worked, and shell dissolution alters exterior and interior surfaces of the shell (Kohn, Myers & Meenadski 1979). In muricids a set of teeth or thickenings on the inner margin of the outer lip is developed at regular intervals. As growth proceeds, these teeth come to lie within the aperture and are resorbed (Vermeij 1978b). Resorption of part of the surface of the penultimate whorl in 'prosobranchs', such as *Trochus*, *Rhinoclavis*, *Strombus* and *Terebra* species may provide fresh surface on which shell material is more easily deposited and is suggested as an adaptive precursor to other types of shell resorption (Signor 1983).

The internal shell cavity in the Neritidae, Turritellidae, *Olivella*, Conidae and Ellobiidae is modified through resorption. Vermeij (1988) suggested that resorption not only produces space that accommodates a large visceral mass, but permits the evolution of the narrowly elongate, toothed aperture in *Nerita* and *Olivella*. As the *Conus* shell grows, profound internal shell dissolution occurs (Fig. 14.6E), and the wall of the protected penultimate whorl may be reduced from several millimetres in thickness to less than 50 μm (Kohn *et al.* 1979) while shell material is added to the inside of the spire and the anterior part of the columella. The resulting shell has a uniformly thick last whorl, a thickened spire that enhances defence against crushing predators, and expanded living space (Kohn *et al.* 1979). In the pulmonate ellobiids, shell resorption involves both the columellar pillar and internal partitions (Fig. 14.6B, D). In other gastropods, such as truncatellids, caecids (Fig. 14.6F–H) and clausiliids, the apical whorls are discarded.

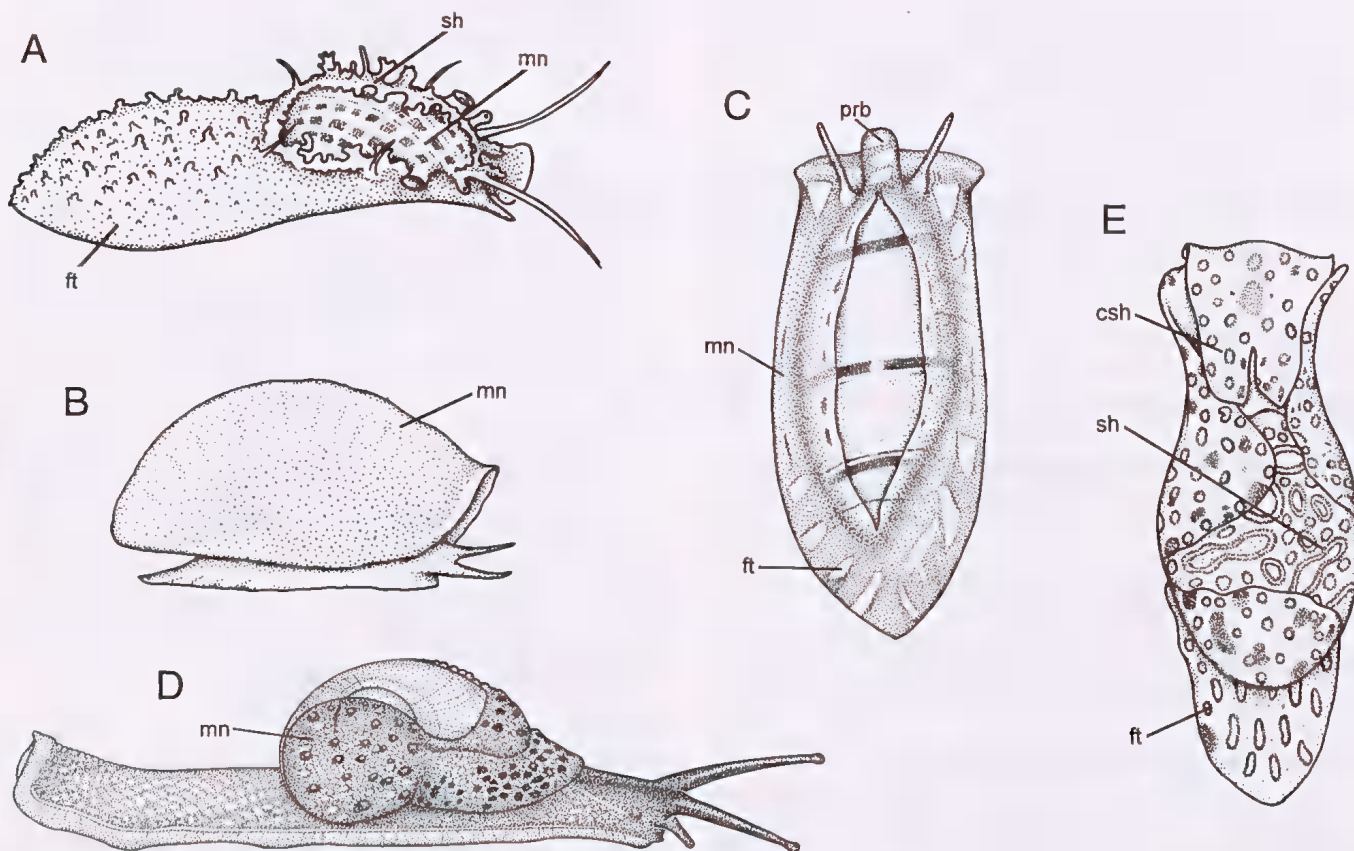


Figure 14.7 Internalisation of the shell. A, a trochid, *Gena strigosa* (Stomatellidae). B, a caenogastropod, *Lamellaria perspicua* (Velutinidae). C, a neogastropod, *Volvarinella cairoma* (Marginellidae). D, a pulmonate, *Fastosarion aquila* (Helicarionidae). E, a cephalaspidean opisthobranch, *Haminoea cymbalum* (Haminoeidae). csh, cephalic shield; ft, foot; mn, mantle; prb, proboscis; sh, shell. (A, after Hedley 1917; B, after Thompson 1976; C, after Ponder 1970; D, after photograph by Queensland Museum; E, after Rudman 1971b) [A–C, E, M. Thompson; D, C. Eadie]

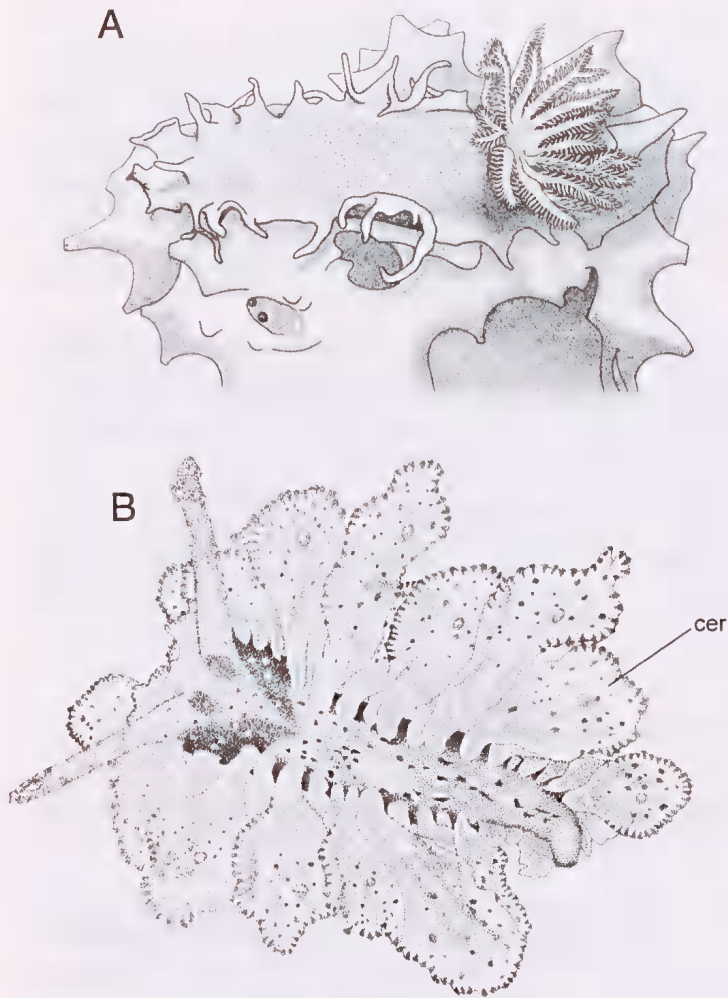


Figure 14.8 Molluscs without a shell. A, the nudibranch *Verconia verconis* (Chromodorididae) on its sponge host. B, *Cyerce* sp. (Caliphyllidae), a sacoglossan with flat, leaf-like cerata. cer, cerata. (After photographs by C. Bryce)

defence. In his review of 58 Australian chromodorids species, Rudman (1991) described the occurrence of sympatric groups of similarly coloured, but unrelated species, and the elaboration of mantle glands containing anti-feedant chemicals. Autotomy of parts of the body is suggested as a compensatory mechanism for the lack of a shell; in the Dorididae parts of the mantle may be lost, and the sacoglossan genus *Cyerce* (Fig. 14.8B) is well known for autotomy of its cerata. In aeolid nudibranchs, stinging capsules from cnidarians in the diet are used defensively (Edmunds 1966).

Perhaps the best-known defence mechanism in shell-less opisthobranchs is that involving the chemicals they produce. Sea hares have been known for their toxic products for more than 2000 years. Recently, a cause and effect relationship between loss of shell and chemical defence mechanisms has been proposed (Faulkner & Ghiselin 1983).

Numerous studies in the laboratories of natural products chemists have elaborated on the many and peculiar chemicals of opisthobranchs. The herbivorous aplysiids (Faulkner & Ireland 1977) and carnivorous dorids (Schulte & Scheuer 1982) can sequester a variety of secondary metabolites from their food – from algae in aplysiids, and from sponges and bryozoans in dorids. These metabolites are then used as defensive allomones. Not all allomones are prey-derived, however. At least one dorid and several pleurobranchs appear to synthesise their chemical defences. Cimino, De Rosa, De Stefano, Sodano & Villani (1983) have established that the allomone polygodial is synthesised by the dorid *Dendrodoris limbata*, stored in the mantle, and then released. Pleurobranchs which lack an external shell appear to synthesise acidic allomones, whereas those with a shell lack this ability (Thompson 1986).

Chemical and mechanical defence mechanisms are also known in terrestrial gastropods both with and without shells. Many slugs produce distasteful mucus (Runham & Hunter 1970). Garlic snails, *Oxychilus* species, are well known for their offensive odour (Lloyd 1970), and an irritating frothy liquid is produced by Florida land snails, *Liguus* species, when they are disturbed (Eisner & Wilson 1970). Self-amputation of the tail in slugs of the genus *Prophysaon* is also suggested as a defence mechanism (Pilsbry 1948).

Gastropods Without Shells

Internalisation of the molluscan shell has occurred several times among gastropods, in both aquatic and terrestrial taxa (Fig. 14.7). The shell is entirely covered by the mantle in the caenogastropod *Lamellaria* (Fig. 14.7B). In other caenogastropods, such as in *Cypraea*, *Natica* and *Oliva*, the mantle entirely covers the shell when the animals are moving, but the animal can be retracted wholly into the aperture. When moving, naticid gastropods internalise the shell by enveloping it with foot and mantle. As a result they become bilaterally symmetrical when in motion, with a low centre of gravity, a small frontal cross section and a low pressure point (Linsley 1977). In some terrestrial groups, for example, the Helicarionidae, the shell is markedly reduced in size and weight and is partially internalised (Fig. 14.7D).

Cephalaspideans such as *Haminoea* have similar morphology and habits (Fig. 14.7E), and there has been a general trend towards loss of the shell in the Opisthobranchia, culminating in more than 20 opisthobranch families in which the members have no shell at all (Fig. 14.8). Loss of the shell has been compensated for by such adaptations as autotomy, camouflage, and the presence of defence mechanisms involving substances either derived from food or synthesised by the animal itself.

Nudibranchs exhibit these three forms of adaptation superbly. Brightly coloured dorids are invisible against their sponge hosts (Fig. 14.8A), while others are mottled, resembling the background on which they live, and some exhibit warning colours. Chromodorids, in addition to colour, remove anti-feedant chemicals from the sponges on which they feed, sequestering these compounds in their own tissues and using them as an anti-feedant

MUSCULATURE AND LOCOMOTION

Hydrostatic Skeleton

Gastropods are soft-bodied animals, but when a snail crawls on a horizontal surface its shell and contained viscera are erect over the head-foot, its tentacles are extended, and muscular waves pass along the foot (Fig. 14.9). Its skeletal support is the blood which, contained in the haemal spaces, provides an effective hydraulic skeleton against which the muscles can operate during locomotion.

Fluid pressures are involved in a variety of movements in gastropods, including extension of siphons, copulatory organs, and protrusion of the complex feeding apparatus. The extension of the head and feeding apparatus is produced by shifting blood into a large cephalopedal (head-foot) sinus equipped with special membrane barriers that keep the blood in the required position (Jones 1975). Remarkable changes in body shape are possible because of the haemal spaces and hydrostatic skeleton. Thus snails and slugs can squeeze into small spaces, slither around rocks, and burrow into sand, soil, and calcareous rocks. Aquatic snails live in a medium which is much denser than air and thus receive considerably more support from their environment than do terrestrial snails. Significantly, they have lower blood pressure than do terrestrial snails (Jones 1975).

In some gastropod structures, such as the tentacles of a limpet which are retracted relatively quickly and extended slowly, the skeletal support provided by a fluid column in the classical hydrostatic skeleton is replaced by a mass of antagonistic muscle in a muscular hydrostat (Marshall, Hodgson & Trueman 1989).

14. CLASS GASTROPODA



Figure 14.9 Direct locomotor waves in gastropods. A, a monotaxic locomotor wave pattern in *Helix* sp. (Helicidae). B, an alternate or ditaxic locomotor pattern in *Pomatias elegans* (Pomatiasidae), in which the entire left and right halves of the foot move alternately. C, alternate locomotor pattern in *Haliotis* sp. (Haliotidae), in which two attached areas and one area moving forward on one side alternate with two moving areas and one attached area on the other side. Shading indicates areas moving forward as muscle contracts; in non-shaded areas the muscle is relaxed and the foot is at rest. Arrows indicate the direction of locomotor waves. (After Morton 1979) [M. Thompson]

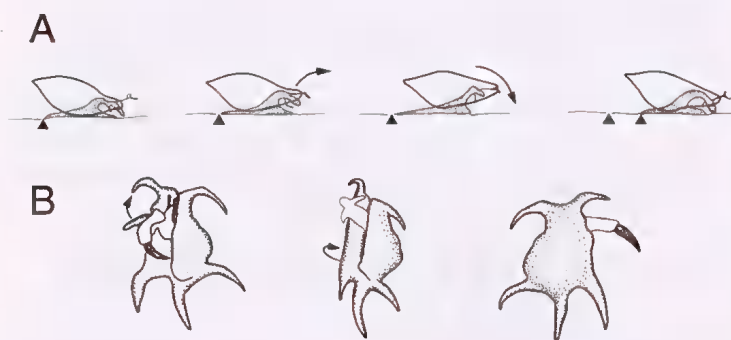


Figure 14.10 Locomotion in the family Strombidae. A, forward movement by thrusting forward abruptly, and subsequent retraction of the rear part of the foot in *Strombus maculatus* (Strombidae). B, righting response in *Lambis chiragra* (Strombidae). Arrows indicate direction of movement. (After Berg 1974) [M. Thompson]

Locomotion

Although most gastropods travel at the proverbial snail's pace, many are remarkably mobile animals.

Forward locomotion in most gastropods is the result of waves of muscular contraction passing along the sole of the foot, but there are many variations on the generalised scheme. The terminology has been summarised by Miller (1974). Waves that travel in the same direction as the animal (posteriorly to anteriorly) are termed direct (Fig. 14.9A). Those moving in the opposite direction are retrograde. If the waves extend across the foot they are monotaxic, or ditaxic if the foot is functionally divided down the middle and waves traverse each side separately (Fig. 14.9B).

The pace of a snail using muscular contraction of the foot is a function of the speed with which the muscles contract and the amplitude of the ripples (Miller 1974). In general, extra speed is achieved by the increase in ripple size which may be out of phase, and in the extreme case, the two sides of the foot step alternately (Fig. 14.9B, C).

Rate of motion also correlates with shell form (Linsley 1978a). In general, the more ornate the shell, the slower the snail, and the more streamlined the shape, the faster the snail. Streamlining is partly dependent on the way the shell is carried during locomotion. Two processes, inclination and regulatory detorsion, move the centre of gravity over the midline of the foot. In low-spired forms, such as *Haliotis* (Fig. 14.4B), the centre of gravity and cross-sectional area are low and the snail moves on a hard substratum at relatively high speeds but it cannot withdraw into the shell. Gastropods with spires of medium height, such as trochids, move more slowly.

Movement by cilia, which has been described for all three classes of gastropods, is characterised by the lack of any visible pedal waves, the even adherence of the entire sole of the foot to the substratum, and uniform gliding of the body (Audesirk 1978). A top speed by ciliary locomotion of 1.9 mm/sec has been recorded in *Tritonia* (Audesirk & Audesirk 1985); speeds achieved by ciliary locomotion are generally two to three times those reached using muscular contraction. However, ciliary movement has its limitations. Small gastropods glide easily using the cilia on the ventral surface of the foot, however, they cannot move backwards and the locomotor power of cilia is inadequate in large animals.

Form and Function in the Gastropod Foot

The gastropod foot is a remarkably versatile organ, and gastropods not only crawl and burrow, but they also swim, leap and stomp. The foot is also used for righting the upturned animal (Fig. 14.10B).

The habit of burrowing in sand has been adopted in at least 20 families of aquatic gastropods across the group (Trueman & Brown 1993). Sand-burrowing gastropods have in common a wedge-shaped or ploughshare-like foot. The foot is extraordinarily expandable in the sand-living Naticidae (Fig. 14.7D). Morris (1950), working on the Australian species, *Polinices sordida*, provided evidence that water uptake was associated with foot expansion. Experiments in the North American *Polinices duplicatus* show that pedal water-sinuses are inflated by intake of seawater that can increase an animal's contracted weight by three and a half times (Russell-Hunter & Russell-Hunter 1968). On retraction of the foot the contained water is ejected. The foot is modified as a head-shield in burrowing caenogastropods such as naticids and in some cephalaspidean opisthobranchs (Fig. 14.7), and acts essentially as a mucous-covered plough and creates a measure of streamlining.

Strombids are 'leapers' (Linsley & Yochelson 1973). In the genera *Strombus* and *Lambis*, the animal thrusts its foot against the substratum, lifting the shell which then falls forward (Fig. 14.10; Berg 1974). The motion is sudden and discontinuous, presumably the result of contraction of the circular muscles. Another unique set of discontinuous movements occur in the surf-living terebrid, *Hastula inconstans*, of Hawaii, which uses the foot as a sail as well as a plough (Fig. 14.11; Kornicker 1961; Miller 1975). The sail effect may be a behavioural adaptation which enables the animals to move rapidly up and down on a high energy beach while feeding (Miller 1975). At least two species of the nassariid genus *Bullia* in South Africa are also intertidal surfers. The propodium is extended, the animal is anchored and the metapodium is dilated, resulting in a stepping motion; the metapodium is then anchored and the cycle is repeated. Trueman & Brown (1989) described the performance as 'superior to *Terebra*', but *Bullia* species also employ a water jet from the mantle cavity which facilitates movement.

Swimming is widespread in opisthobranchs, perhaps facilitated by the fact that the shell is reduced or absent in many. Three categories are identified (Farmer 1970). The simplest swimming pattern is that of the Spanish dancer, *Hexabranchius sanguineus*, in Australia, which involves a series of dorso-ventral flexions of the body wall musculature. A modified undulation involving only

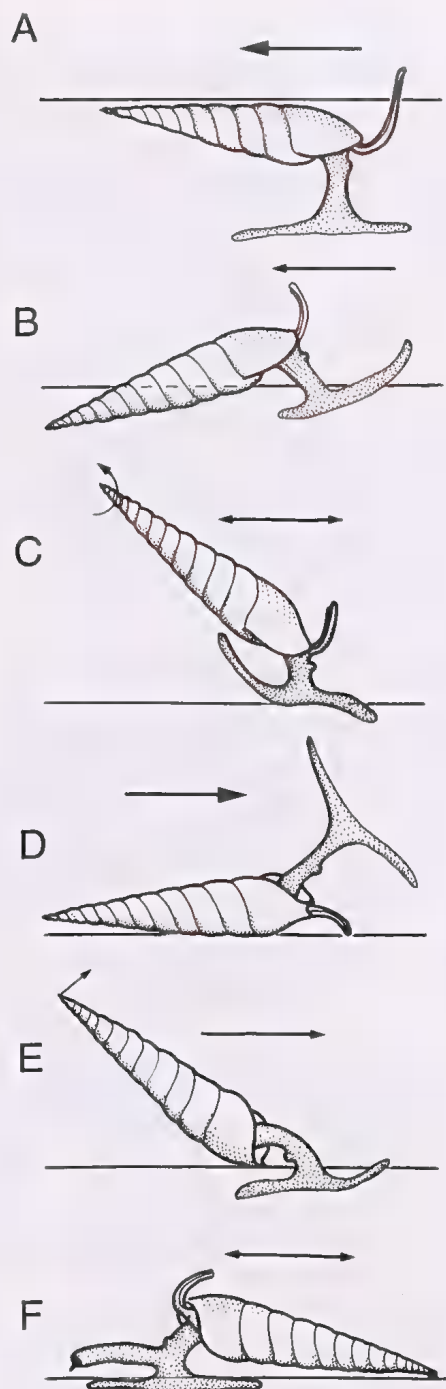


Figure 14.11 Movement in the terebrid, *Hastula inconstans* (Terebridae), showing the sail effect: A, buried in sand with an incoming wave passing; B, crawling to the sand surface; C, apex of shell raised; D, with the foot as a sail, the animal is carried seaward by the outgoing wave; E, propodium digging into the sand; F, prey search before the next incoming wave. Arrows indicate the direction of water flow. (After Miller 1979) [M. Thompson]

lateral bending is used by *Melibe leonina*, especially in the presence of noxious stimuli (Hearst 1968) and may be a means of escape (Thompson 1976). *Aplysia brasiliana* swims by moving its parapodia which have a large surface area and thereby maintain the sea hare in the water column (Kandel 1979); swimming appears to be an effective means of local movement (Hamilton & Ambrose 1975).

The gastropod foot is also adapted to pelagic life in a few groups. In the heteropod prosobranchs the foot is drawn out into a highly mobile fin. This is held upward in *Carinaria*, which swims upside down (see Fig. 15.146). In the pteropod genus *Clione*, the base of each parapodium is narrow, allowing twisting at that point during both upward and downward beats so as to increase the power of

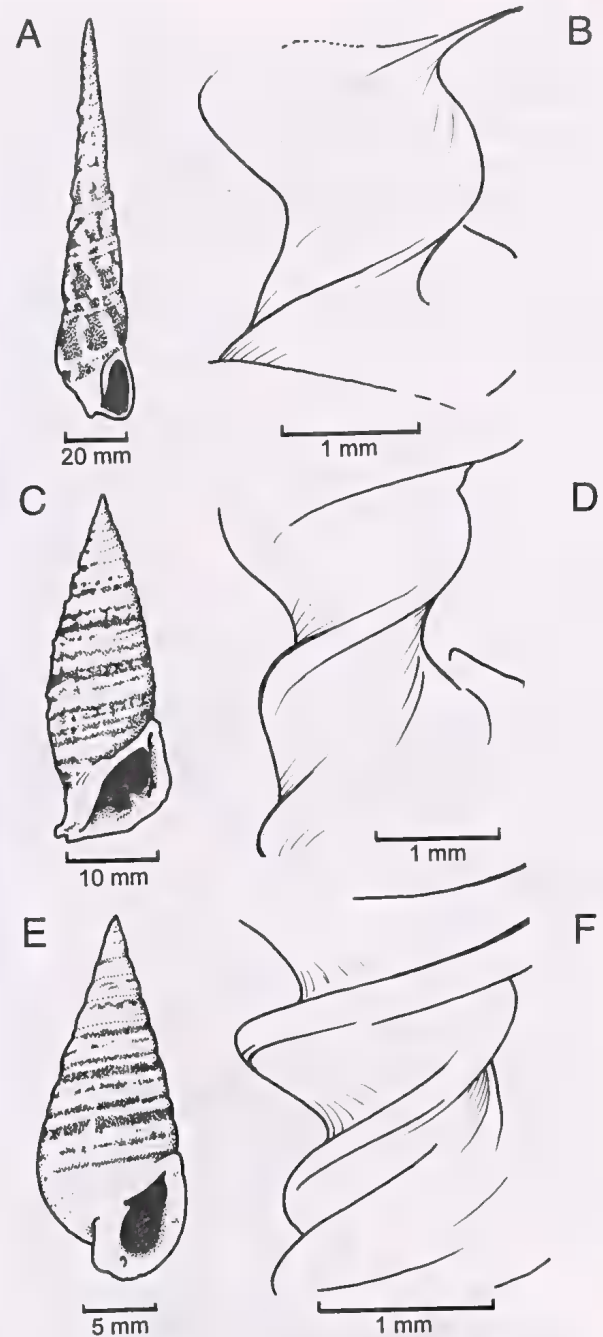


Figure 14.12 Turritelliform gastropod shells (A, C, E) and columellar folds (B, D, F). A, B, *Terebra dimidiata* (Terebridae). C, D, *Rhinoclavis aspera* (Cerithiidae). E, F, *Pyramidella dolabrata* (Pyramidellidae). (After Signor & Kat 1984) [M. Thompson]

their stroke in both directions. Air bubbles trapped in the anterior part of the foot of species in the caenogastropod genus *Janthina* form a float (Pl. 24.4; Wilson & Wilson 1956).

Shell Shape and Locomotion

Many gastropods balance the shell on the cephalopodal mass and crawl during much of their life. A few have open coiled shells and lead sedentary lives, as in *Siliquaria* (Fig. 14.4H). Architectonicids (for example, species of *Architectonica* and *Philippia*) are also rather sedentary gastropods and have shells with radial apertures, that is, the plane of such apertures includes the axis of coiling of the shells (Linsley 1978a). In some gastropods such as *Cerithium* and *Conus*, the 'sides' of the shell rest on the substratum with the axis of coiling parallel to the substratum. Very high spired or turritelliform snails, such as *Terebra*, drag the shell (Linsley 1977, 1978a; Miller 1979). As these snails move, the foot advances, stops, and the shell is drawn forward by the columellar muscle. Presence or absence of columellar folds is one of the best predictors of the mode of life among modern turritelliform species.

They are present in burrowing groups such as terebrids (*Terebra*) (Fig. 14.12A, B), cerithiids (*Rhinoclavis*) (Fig. 14.12B, C), and pyramidellids (*Pyramidella*) (Fig. 14.12E, F). The adaptive features of the columella, the single internal structure in a gastropod shell, have been demonstrated recently. Signor & Kat (1984) showed that turrilliform gastropods with folds on the columella are burrowers (Fig. 14.12), and suggested that the columellar folds prevent lateral shifting of the columellar muscle when the mantle is contracted.

NERVOUS SYSTEM AND SENSE ORGANS

Nervous System

Gastropods are usually thought of as slow-moving, rather unresponsive animals. Recent studies, however, suggest they are neither uncoordinated nor unresponsive to environmental cues. Indeed, the sophistication and complexity of gastropod behaviour are being recognised only now (Audesirk & Audesirk 1985).

The large ganglia and relatively simple structures of opisthobranchs and pulmonates are proving useful in neuro-ethological systems (see Audesirk & Audesirk 1985 for a review). Specific identifiable neurons in gastropod brains control complex orientation responses, feeding movements and activity rhythms by precisely known motor pathways and networks. Gastropods are increasingly important as model systems for neurobiological studies of learning and memory and are providing the first cellular-level explanations of the relationships between neuronal plasticity and complex behavioural plasticity (Kohn 1983).

Central Nervous System

The gastropod central nervous system includes five groups of paired ganglia associated with the buccal structures, various head organs such as the tentacles, and rhinophores (in opisthobranchs), the foot, the visceral mass, and the mantle (Fig. 14.13A). These five pairs of local 'brains', the cerebral, buccal, pleural, pedal and oesophageal ganglia, and an unpaired visceral ganglion, are linked by connectives and commissures (Fig. 14.13A). As a result of torsion the visceral loop, consisting of the visceral and oesophageal ganglia and their connectives, are crossed in the streptoneurous groups and secondarily untwisted in opisthobranchs and pulmonates (the euthyneurous groups; Fig. 14.13B, C).

In the Opisthobranchia, the connectives are shortened, and the animal is essentially bisymmetrical. All the ganglia lie in the nerve ring, usually above the oesophagus, and are united only by the pedal commissure (Fig. 14.13B). Pulmonates regained symmetry primarily by a shortening of the connectives and ganglionic fusion (Kandel 1979). These molluscs have the most consistently concentrated gastropod nervous system, comprising a thick circumoesophageal ring of paired ganglia.

Sensory Receptors and Responses

Gastropod sensory receptors include eyes, tentacles, rhinophores (only in opisthobranchs), osphradium and mantle papillae. The eyes and some papillae are well known to be light sensitive, and a suite of structures, including the rhinophores of opisthobranchs, anterior mantle papillae and osphradium, serve as chemoreceptors (Kohn 1961). The rhinophores and osphradia resemble mammalian olfactory organs and other chemoreceptors such as neuroepithelial

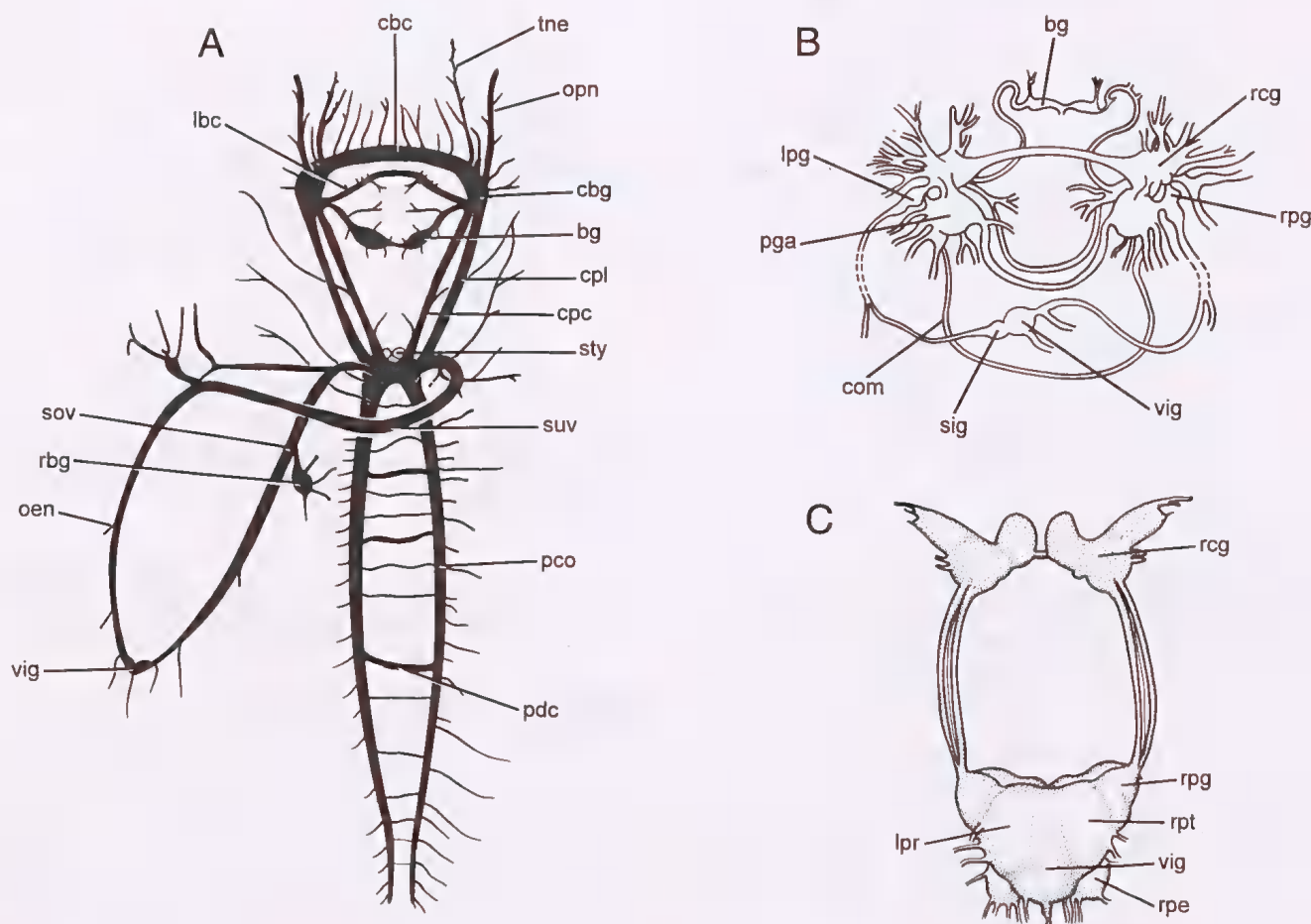


Figure 14.13 Nervous systems of some gastropods. A, the vetigastropod, *Haliotis tuberculata* (Haliotidae). B, the opisthobranch, *Philine aperta* (Philinidae). C, a pulmonate, *Helix* species (Helicidae). bg, buccal ganglion; cbc, cerebral commissure; cbg, cerebral ganglion; com, commissure; cpc, cerebropleural connective; cpl, cerebropleural connective; lbc, labial commissure; lpg, left pleural ganglion; lpr, left parietal ganglion; oen, oesophageal nerve; opn, optic nerve; pco, pedal nerve cord; pdc, pedal commissure; pga, pedal ganglion; plg, pleural ganglion; rbg, right branchial ganglion; rcg, right cerebral ganglion; rpe, right pedal ganglion; rpg, right pleural ganglion; rpt, right parietal ganglion; sig, subintestinal ganglion; sov, suboesophageal part of the visceral loop; sty, statocyst; suv, supra-oesophageal part of visceral loop; tne, tentacular nerve; vig, visceral ganglion. (A, after Fretter & Graham 1962; B, after Thompson 1976; C, after Kerkut & Walker 1975)

[M. Thompson]

cells or free nerve endings (Kohn 1961). The osphradium, a distance chemoreceptor concerned with food recognition and location, is reviewed by Taylor & Miller (1989). It varies among caenogastropods from a simple, elongate ridge to a complex bipectinate or tripectinate structure. In algal and deposit-feeders such as *Littorina* it consists of a simple ridge; the osphradium of *Rhinoclavus* bears leaflets, and in predators like *Conus* the margins of the leaflets are folded and digitate. Haszprunar (1985a, 1985b) has investigated the fine structure of the osphradium in detail. The primary chemosensory neurons, with peripheral somata, are located beneath the sensory epithelium or in peripheral ganglia.

It has long been held that gastropod eyes are useful only in light versus dark distinctions. A classic example is the shadow response of the pond snail, *Lymnaea stagnalis*, which withdraws when light decreases suddenly. Recent evidence suggests that this response is controlled by sites of extraocular photoreception rather than being visually mediated (Audesirk & Audesirk 1985). However, more complex responses may be mediated via the eyes. For example, it has been suggested that response by the eyes is involved in phototaxis in the land snail genera *Helix* and *Otala*. Several gastropods also behave in ways that appear to require at least rudimentary forms of vision, combined with an internal representation of certain important features of the environment (Hamilton 1977). Orientation of littorinids to vertical grass stalks and the apparent orientation swimming in *Aplysia brasiliana* in response to celestial cues argue for some visual acuity (Hamilton 1977; Hamilton & Russell 1982).

Despite the potential for complex visual reception, a gastropod perceives its world primarily by chemoreception (Kohn 1961; Audesirk & Audesirk 1985). Chemical senses govern a wide range of behaviours in gastropods; examples are the identification of potential food sources, the initiation of feeding, detection of predators and noxious stimuli, the identification and location of conspecifics in aggregation and mating, and the synchronisation of spawning (Audesirk & Audesirk 1985).

In 'prosobranchs', contact chemoreception has been demonstrated in the cephalic and posterior tentacles of *Nassarius reticulatus* (Crisp 1971). In opisthobranchs these areas include: the tips of the rhinophores and tentacles, and the area around the mouth (*Aplysia*; Preston & Lee 1973); the edge of the oral veil, tentacles, rhinophores and proboscis (*Pleurobranchaea californica*; Lee, Robbins & Palovcik 1974); and the anterior lateral folds, head shield, labial palps and pharyngeal lips (*Navanax*; Murray & Lewis 1974).

Experimentation with choice chambers has shown that various herbivorous gastropods can detect the presence of suitable seaweeds and move in their direction. Behavioural studies demonstrate that some herbivorous, carrion-feeding, and predatory gastropods are attracted by chemical stimuli emanating from food (Kohn 1961). The piscivorous species of *Conus* detect the presence of prey at considerable distance (Kohn 1961). Some of the more agile gastropods respond to chemical emissions from enemies by fleeing. The larva of the dorid *Adalaria proxima* settles and metamorphoses only in the presence of the polyzoan *Electra pilosa* and evidently responds to some chemical emanation from this species (Thompson 1958).

Homing Behaviour

Eroded areas on rocky shorelines often mark the particular place of 'home scars' to which marine limpets consistently return after their normal tidal feeding excursions. Homing behaviour has been described for *Acmaea scabra* (Hewatt 1940; Jessee 1968), *Acmaea digitalis* and *Lottia gigantea* (Galbraith 1965) and *Patella vulgata* (Orton 1929; Cook, Bamford, Freeman & Teideman 1969) among prosobranch limpets, and for the pulmonate limpet *Siphonaria japonica* (Cook 1969). Mackay & Underwood (1977) reported on two eastern Australian samples of *Cellana tramoserica* in which homing behaviour was demonstrated, but other individuals of the same species do not home.

Underwood (1977, 1979) discussed homing in detail, and listed three key aspects of this behaviour that need consideration. Firstly, the return of limpets to home scars must be non-random, that is greater than the proportion that would return to a home site by chance alone. Secondly, several hypotheses have been presented to explain how the limpets return to the home site. The most likely mechanism is that a chemical cue is deposited on the outward journey and is followed on the return journey to the home site. Thirdly, the selective advantages of homing have not been identified for most species. One frequent suggestion is that the limpet shell fits closely to the substratum at the home site, reducing desiccation. Underwood (1979) suggested that this is not the correct explanation as many limpets are not in fact tightly clamped to the substratum at low tide. Underwood (1979) discussed several studies in which homing is considered to be density dependent in providing a feeding area with a suitable food supply for each limpet.

Learning

Learning, defined as any behavioural change resulting from the experiential history of the animal, is now well studied in gastropods (for a review see Mpitsos & Lukowich 1985).

Gastropods can alter their behaviour appropriately based on experience and can remember what they have learned in a single conditioning trial for up to 28 days (Kohn 1983). The longest period of memory retention reported for a gastropod is four months in *Achatina fulica* (Croll & Chase 1977). In experimental work primarily with opisthobranchs, feeding responses have been modified by experience, including habituation, sensitisation, satiation and associated learning. Non-associated aversive behaviour modification has been demonstrated by Kupferman & Pinsker (1968) who showed that an electric shock applied to the oral veil of *Aplysia californica* inhibits the consummatory feeding response for up to 24 hours. In conditioning experiments, *Pleurobranchaea californica* learnt to associate the touch of a sterile glass rod with contact by food homogenate (Mpitsos & Davis 1973). In *Aplysia*, learning to increase or decrease its reflex responses to certain stimuli does not develop all at once but forms gradually from juvenile to adult, and specific changes in the nervous system can be correlated with the acquisition of new learning capacities during development (Mpitsos & Lukowiak 1985).

MANTLE CAVITY, RESPIRATION, CIRCULATION AND EXCRETION

Mantle Cavity

The mantle cavity, perhaps of all gastropod features, may be the single most important character pre-adapting these molluscs to their great diversity of lifestyles. The mantle epithelium, which secretes the gastropod shell, envelops the visceral mass and hangs from it like a skirt. The mantle or pallial cavity is the space between the mantle skirt and the sides of the body – anterior and forward-facing in post-torsional prosobranchs (Fig. 14.14) and pulmonates (Fig. 14.19) and lateral or posterior in opisthobranchs (Fig. 14.17). It is a space into which the head and foot can be withdrawn. It contains the organs of respiration (gills), circulation (heart), and excretion (kidney), as well as the ducts that carry waste from the gut (rectum) and reproductive cells (genital ducts). In a few taxa it functions as a brood pouch. Two peculiarly molluscan structures, the hypobranchial gland and osphradium are also contained within the mantle cavity (Fig. 14.14). This assortment of structures and functions in gastropods has been described as '... at one and the same time their strength, ... and their weakness, containing a collection of incompatible neighbours ...' (Graham 1948). The cavity, with its 'incompatible neighbours', has proved to be remarkably versatile.

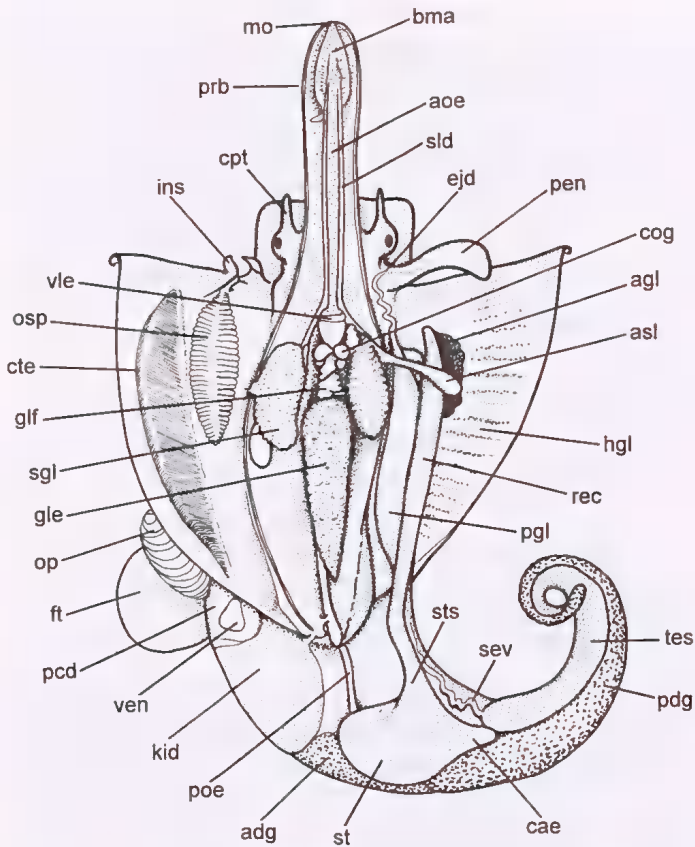


Figure 14.14 The pallial cavity and anterior body cavity (opened and viewed dorsally) of a generalised muricoidean neogastropod removed from its shell and with the proboscis extended. **adg**, anterior lobe of digestive gland; **agl**, anal gland; **aoe**, anterior oesophagus; **asl**, accessory salivary gland; **bma**, buccal mass; **cae**, gastric caecum; **cog**, circumoesophageal ganglia; **cpt**, cephalic tentacle; **cte**, ctenidium; **ejd**, ejaculatory duct; **ft**, foot; **gle**, gland of Leiblein or foregut gland; **glf**, glandular dorsal folds of mid-oesophagus; **hgl**, hypobranchial gland; **ins**, inhalant siphon; **kid**, kidney; **mo**, mouth; **op**, operculum; **osp**, osphradium; **pcd**, pericardium; **pen**, penis; **pdg**, posterior lobe of digestive gland; **pgl**, prostate gland; **poe**, posterior oesophagus; **prb**, proboscis; **rec**, rectum; **sev**, seminal vesicle; **sgl**, salivary gland; **sld**, salivary duct; **st**, stomach; **sts**, style sac region of stomach; **tes**, testis; **ven**, ventricle; **vle**, valve of Leiblein. (After Ponder 1973) [M. Thompson]

The organs in the mantle cavity of the hypothetical primitive gastropod, except for the gonad, are thought to have been paired (Fig. 14.15A); the general trend has been towards increasing asymmetry in renal, reproductive, respiratory and circulatory systems. In all gastropods the gonad is a single opening on the post-torsional right side. A few living gastropods have paired kidneys, although in some vetigastropods, particularly the Fissurellidae, the left kidney is very reduced and eggs and sperm are discharged through the single functional kidney duct (Fig. 14.15B). Patellogastropoda (Fig. 14.15B) and most vetigastropods (Fig. 14.15D) have two functional kidneys, the post-torsional right being the larger. In caenogastropods, Neritopsina (Fig. 14.15E) and heterobranchs, there is a single kidney, the post-torsional left; the right kidney rudiment, however, is incorporated in the genital system in at least the first two of these groups. The left kidney of caenogastropods discharges by way of its own duct or opening, and the ova and sperm are discharged entirely separately by ducts which become enlarged and extended as specialised reproductive organs (Fig. 14.15C), but incorporate the right kidney.

Prosobranch Gills

In all non-euthyneuran gastropods the mantle cavity opens broadly and contains either two ctenidia or a single left ctenidium (Fig. 14.16). This association was used in a classificatory scheme in which the more primitive vetigastropods were termed zygobranchs because of the two ctenidia, and those with a single ctenidium called aspidobranchs. The arrangement seen in fissurellids (Fig. 14.16A) is considered primitive. The paired, feather-like gills are made up of alternating ctenidial leaflets on each side of the axis (a condition called bipectinate) in which run afferent and efferent blood vessels. A respiratory water current is created by lateral cilia on the surfaces of the leaflets. The ctenidia are suspended in the mantle cavity by membranes. This arrangement effectively divides the mantle cavity into two compartments, an inhalant chamber with the osphradium as a water 'taster' and an exhalant chamber into which the anus and urinogenital ducts discharge. The inhalant water current enters the mantle cavity ventrally from both sides and the exhalant current passes out mid-dorsally.

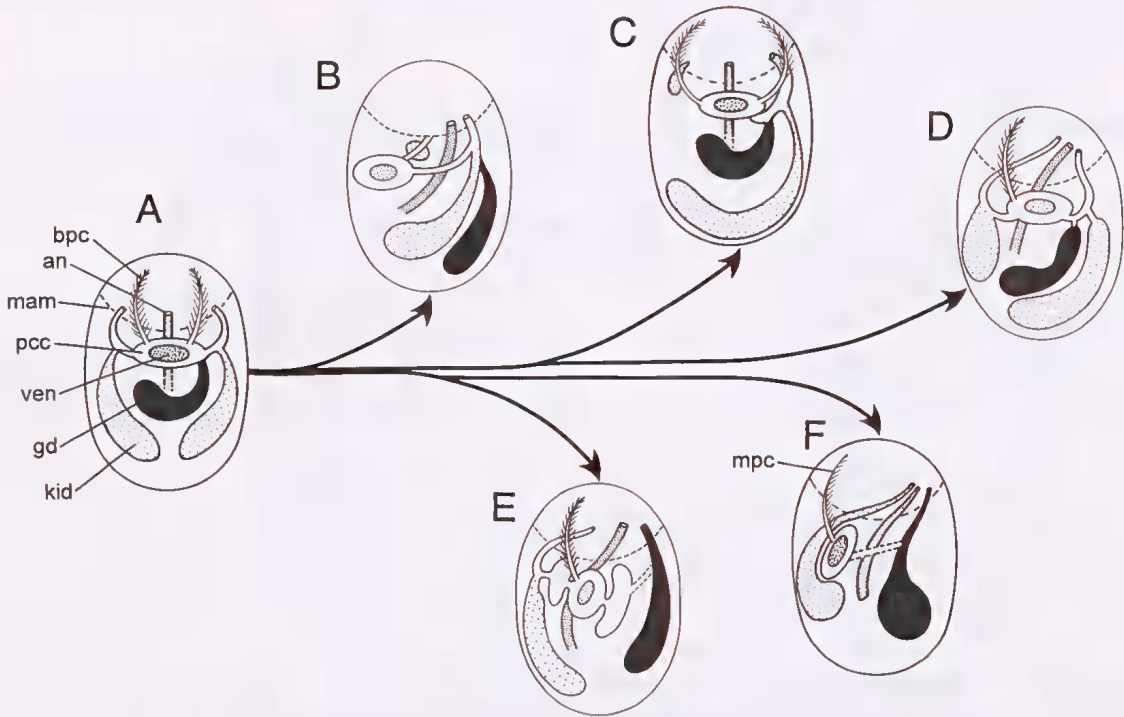


Figure 14.15 The interrelationship of rectum and anus, gonad, pericardial cavity, mantle cavity and ctenidia in Gastropoda. **A**, an ancestral post-torsional mollusc. **B**, a patellogastropod. **C**, a fissurellid (*Diodora* sp.). **D**, a trochid. **E**, a neritospine. **F**, a caenogastropod. **an**, anus; **bpc**, bipectinate ctenidium; **gd**, gonad; **kid**, kidney; **mam**, boundary of mantle cavity; **mpc**, monopectinate ctenidium; **pcc**, pericardial cavity; **ven**, ventricle. (Modified after Russell-Hunter 1979 and Voltzow 1994) [M. Thompson and C. Eadie]

In caenogastropods, the pectinibranch condition (Fig. 14.16B) obtains, whereby the gill is no longer feather-like but comb-like (monopectinate). A single series of filaments extends along the ctenidial axis which is attached to the wall of the mantle cavity. The leaflets have skeletal rods (also present in vetigastropods) and ciliary tracts which maintain a flow of water such that the inhalant water passes from the left side of the mantle cavity through the gill and the exhalant current passes out on the right side instead of over the head of the snail (Fig. 14.16B). The water current passes over the osphradium from the left and the hypobranchial gland and anus on the right. The roof of the mantle cavity usually bears the large, originally left, hypobranchial gland. The mucus from this gland immobilises suspended particles which are then expelled. Paired hypobranchial glands in vetigastropods function in a similar way. This reduction or loss of pallial organs on the right side also took place independently in the Trochoidea, Neritopsina and the patellogastropod and cocculiniform limpets (Haszprunar 1988a; Ponder & Lindberg 1996). In the Patellogastropoda ctenidia have been lost altogether. The mantle edge, which is continuous around the edge of the shell aperture, is the site for gas exchange. This often takes place through

secondary pallial gills, such as those of *Patella* species (Fig. 14.16C; Lindberg this volume). These limpets reduce the risk of contaminating the organs of the mantle cavity by producing compacted faeces which are expelled into the mantle cavity only when the animal is submerged (Purchon 1968).

Opisthobranch Gills

Opisthobranchs also have one or more secondary gills or ctenidia. However, unlike the ctenidium of other gastropods, primitive opisthobranch ctenidia have a narrow attachment to the mantle. They often project from the shallow mantle cavity and always lack skeletal support. In more advanced opisthobranchs the mantle cavity has migrated along the right side and become shallower, such that the head and foot are no longer withdrawn and the secondary gill lies behind the auricle (Fig. 14.17A), from which arrangement the name 'opisthobranch' derives. These changes are accompanied by a reduction in coiling of the visceral mass which now rests on the foot and a reduction of the shell (Fig. 14.17B). In nudibranchs, the most specialised of opisthobranchs, both the shell and mantle cavity are lost.

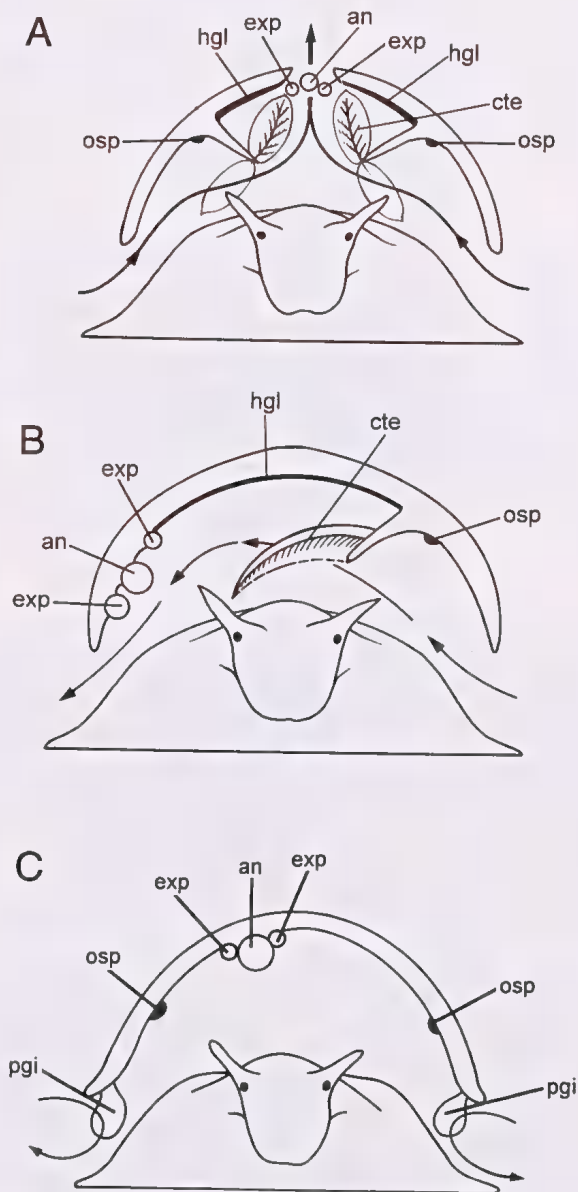


Figure 14.16 The position of mantle cavity organs in relation to the ciliary current in three gastropod groups. A, the Vetigastropoda (*Diodora* sp., Fissurellidae). B, the Caenogastropoda (*Buccinum* sp., Buccinidae). C, the Patellogastropoda (*Patella* sp., Patellidae). **exp**, excretory aperture; **hgl**, hypobranchial gland; **osp**, osphradium; **pgl**, pallial gill. Arrows indicate the direction of the ciliary current. (A, B, after Graham 1948; C, Purchon 1968) [A, B, M. Thompson; C, C. Eadie]

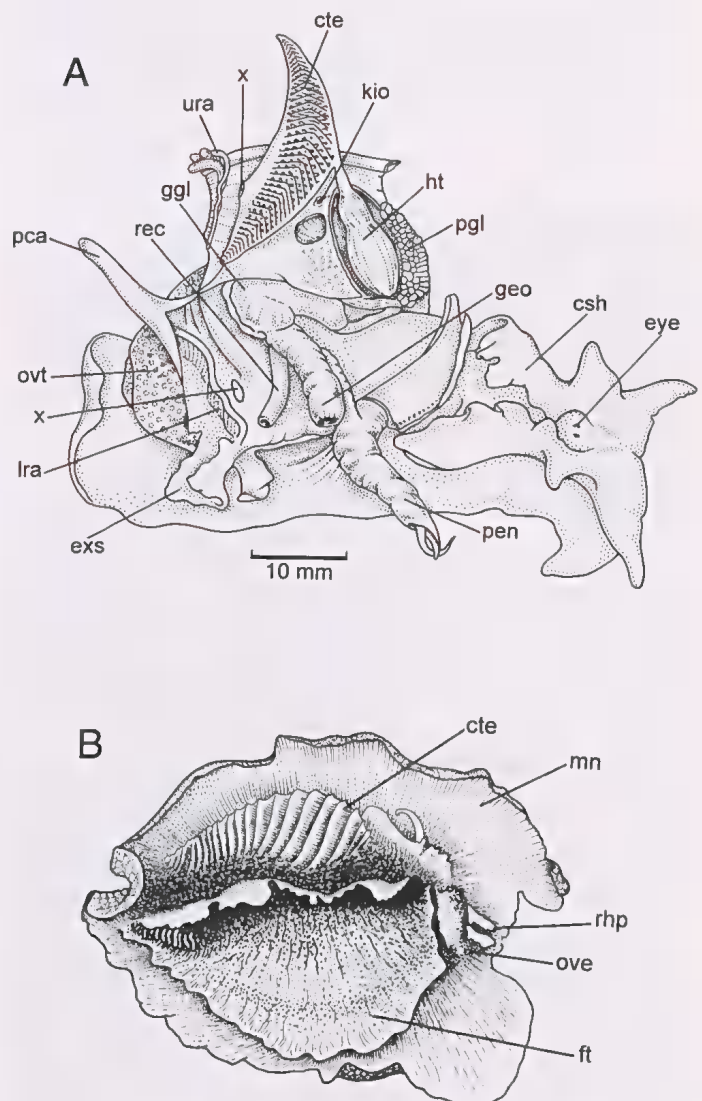


Figure 14.17 The opisthobranch mantle cavity. A, the opened mantle cavity of *Hydatina phtysis* (Hydatinidae) to show the internal organs. B, ventral view of *Oscanus hilli* (Pleurobranchidae), showing the ctenidia lying below the mantle skirt. **csh**, cephalic shield; **cte**, ctenidium; **exs**, exhalant siphon; **eye**, eye; **geo**, genital opening; **ft**, foot; **ggl**, genital gland mass; **ht**, heart; **kio**, kidney opening; **lra**, lower raphe; **mn**, mantle; **ove**, oral veil; **ovt**, ovotestis; **pca**, pallial caecum; **pen**, penis; **pgl**, pericardial gland; **rec**, rectum; **rhp**, rhinophore; **ura**, upper raphe; **x**, point of attachment of ctenidium to mantle cavity floor. (A, modified after Rudman 1972a; B, after Hedley 1894b) [M. Thompson]

14. CLASS GASTROPODA

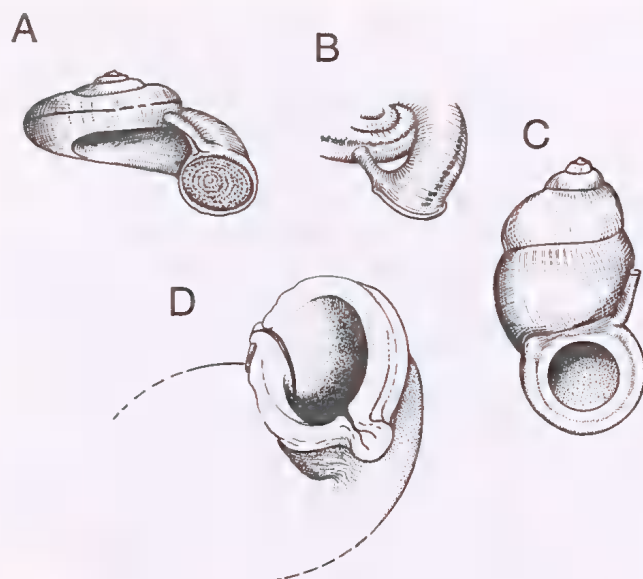


Figure 14.18 Breathing tubes of terrestrial prosobranchs. **A, B**, the breathing tube of *Rhiostoma housei* (Cyclophoridae), from Thailand, is incompletely formed and its aperture is protected by the adjacent preceding whorl. **C**, the complete sutural tube in *Rhiphaulus chrysalis*, a Burmese pupinid, leads to an internal groove inside the mouth of the shell. **D**, *Pupinella simplex* (Pupinidae) from Queensland, in which a notched groove on the columellar wall extends backward and a second notch on the margin of the aperture forms a supplementary breathing pore. (A, B, D, after Rees 1964; C, after Solem 1974a) [M. Thompson]

Freshwater and Terrestrial Gastropods

Only some caenogastropods, neritopsines and pulmonates have invaded both freshwater and land. The operculum, retained in both freshwater and terrestrial caenogastropods and neritopsines, aids in survival during drought conditions, but many other adaptations have evolved during the radiation of both freshwater and terrestrial groups.

Freshwater caenogastropods and neritopsines are ctenidial breathers and have various devices to ensure water flow. The large Ampullariidae, which do not occur in Australia except as aquarium animals, use either a gill or breathe air into a separate lung through a long siphon-like tube formed from part of the mantle collar. The ability to breathe in two ways is apparently advantageous in members of this group, which frequently inhabit tropical canals or swamps with waters low in oxygen during much of the year.

Terrestrial caenogastropods and neritopsines lack gills, and respiration occurs on the inner surface of the highly vascularised mantle. In most groups, water excreted by the kidney keeps the interior of the pallial cavity moist. Faecal pellets are expelled at the right anterior margin of the pallial cavity (Solem 1974a). During extreme conditions, the snail can retreat behind its operculum which can form an effective apertural seal. In some taxa, notches, grooves, slits and tubes provide for oxygen and carbon dioxide exchange between the environment and the pallial cavity, even when the snail is retracted (Fig. 14.18). In the Australian pupinid, *Pupinella simplex*, a notched groove on the columellar wall extends some distance backwards, while a second notch on the upper margin of the aperture provides a shallow, supplementary breathing pore if the snail is retracted only slightly (Fig. 14.18D; Solem 1974a).

The movement of one very ancient group of gastropods from an aquatic habitat to a terrestrial one required a major adaptive shift involving a series of innovative structural modifications. One of these modifications was the isolation of the mantle cavity from the external environment and vascularisation of the roof, providing for air breathing. The name of this group, the 'Pulmonata', is derived from the Latin *pulmo*, meaning lung.

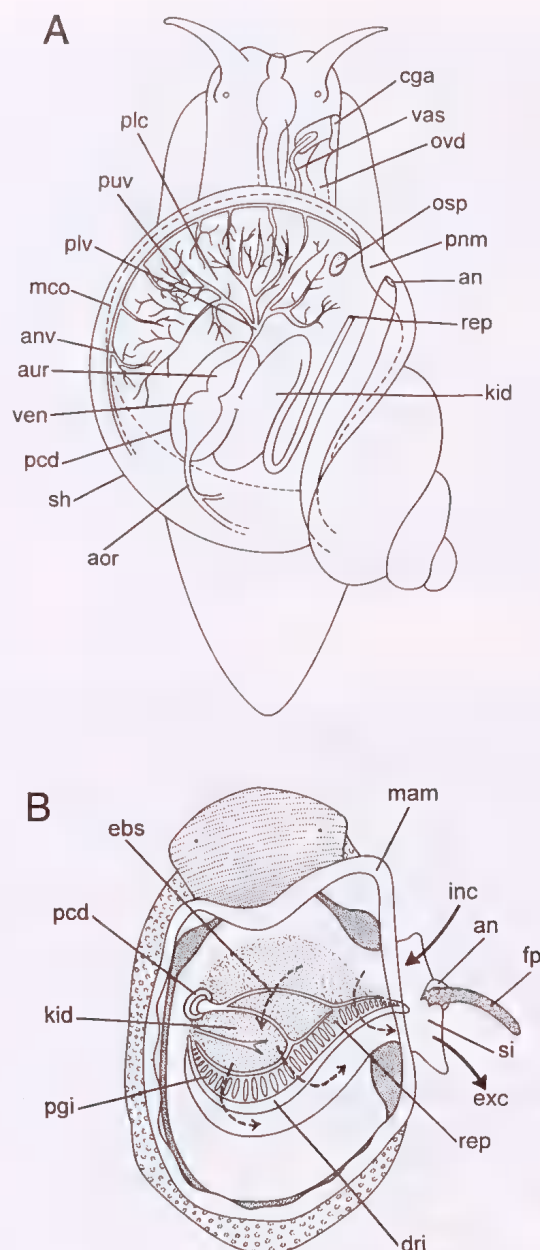


Figure 14.19 The pulmonate mantle cavity. **A**, a freshwater basommatophoran snail. **B**, a dorsal view of *Siphonaria alternata* (Siphonariidae), with the shell removed to show the mantle cavity. Arrows indicate the flow of water over the pallial gills. **an**, anus; **anv**, annular vein; **aor**, aorta; **aur**, auricle; **cga**, common (hermaphrodite) genital aperture; **dri**, dorsal ridge; **ebs**, efferent branchial vein; **exc**, exhalant current; **fp**, external discharge of faecal pellets; **inc**, inhalant current; **kid**, kidney; **mam**, mantle margin; **mco**, mantle collar; **osp**, osphradium; **ovd**, oviduct; **pcd**, pericardium; **pgl**, pallial gill; **plc**, pulmonary cavity; **plv**, pulmonary vein; **pnm**, pneumostome; **puv**, pulmonary vessels; **rep**, renal aperture; **sh**, shell; **si**, siphon; **vas**, vas deferens; **ven**, ventricle. (A, after Cox 1960b; B, after Purchon 1968) [C. Eadie]

In the Pulmonata, the 'lung' is a pallial cavity (Fig. 14.19B) which is derived from the fusion of most of the mantle margin with the dorsal surface of the body. Major organs of the original gastropod mantle cavity, such as the ctenidia and hypobranchial gland, are no longer present. Other structures are modified. Gas exchange occurs through the highly vascularised roof via a network of capillaries. Air enters and leaves through a small opening on the right side, the pneumostome, and is renewed by the pumping action produced by the alternate contraction and relaxation of the muscular floor.

Aquatic pulmonates include primitive, marine littoral and supralittoral families, such as the Ellobiidae, Amphibolidae, Otinidae, Siphonariidae and Trimusculidae, as well as the Lymnaeidae and Physidae of streams and lakes, and the freshwater limpets, Ancyliidae. Some forms have secondary gills, and in others which lack gills the mantle cavity retains a

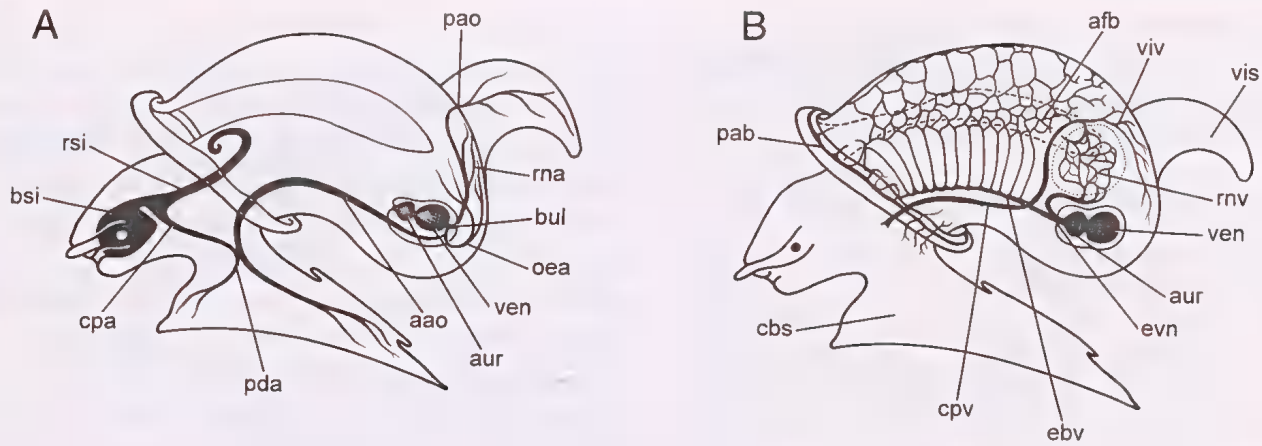


Figure 14.20 The circulatory system of the caenogastropod *Littorina littorea* (Littorinidae), diagrammatic representation, left view. A, the basic arterial system. B, the basic venous system. The main blood sinuses are stippled. aao, anterior aorta; afb, afferent branchial vessel; aur, auricle; bsi, buccal sinus; bul, bulb of aorta; cbs, cephalopodal blood sinus; cpa, cephalic artery; cpv, cephalopodal vein; ebv, efferent branchial vessel; evn, efferent vessel from nephridial gland; oea, oesophageal artery; pab, pallial blood sinus; pao, posterior aorta; pda, pedal artery; rna, renal artery; rnv, renal vessels; rsi, radular sinus; ven, ventricle; vis, visceral sinus; viv, visceral vein. (After Fretter & Graham 1962) [M. Thompson]

secondary function as a lung (McMahon 1983). A variety of air-getting adaptations are associated with the aquatic life of these forms. Some of the lymnaeids of Europe, for example, surface at regular intervals and are restricted to the edges of shallow water bodies. Others have a gas bubble in the lung containing 84% nitrogen, which is used as a 'physical gill' for extracting oxygen from the water by diffusion (Ghiretti 1966a; Russell-Hunter 1978).

Circulation

The gastropod circulatory system is unusual in two ways. Although gastropods, like all molluscs, are coelomate, the body cavity *sensu stricto* is reduced merely to the pericardium which encloses the heart. Secondly, the kidney and its blood vessels play an important role in circulation. The morphological consequences of the body cavity arrangement are reflected in the presence of three major venous sinuses: the cephalopodal sinus, the visceral sinus (Fig. 14.20B), and the subrenal sinus which lies near the columellar muscle at the base of the visceral mass. A functional consequence of this arrangement is the effective hydrostatic skeleton described above.

In most gastropods the circulatory system comprises a central, contractile heart – one or two auricles and a ventricle – linked to the various parts of the body by arteries and veins (Fig. 14.20A). The arteries and veins are connected by small capillary-like channels, and by the venous sinuses. The heart consists of a single, muscular ventricle and one or two thin-walled auricles. In one early system of classification, the gastropods with one auricle – caenogastropods, neogastropods, opisthobranchs and pulmonates – were designated the Monotocardia, and those with two auricles – such as *Patella* and *Halotis* – were termed the Diotocardia. The single auricle in the Monotocardia corresponds to the left auricle of diotocardiids; both receive blood from the left ctenidium and left kidney.

The heart is a systemic pump. Blood flowing into the auricle from the gills, kidney and venous sinuses is actively pumped by the ventricle into the major anterior and posterior blood vessels. Back-flow is prevented by valves. The cephalopodal sinus drains blood from the head and foot, and blood flows back from the visceral mass to the visceral sinus. Blood is distributed through the respiratory organs and the kidney from the subrenal sinus before returning to the heart. All or part of the venous blood may flow also into an extensive renal portal system.

The molluscan heart is myogenic (Jones 1983), that is, the pacemaker action potential is initiated within the heart. It beats rhythmically and spontaneously in isolation and when denervated, as shown by studies of sea hares in the genus *Aplysia*, and of the land snail genus *Helix*, in which the denervated heart functions for a considerable period of time (Jones 1983).

The principal respiratory pigment in gastropods is haemocyanin (Ghiretti 1966b). This copper-containing compound has similar oxygen-carrying capacities to haemoglobin, but tends to be saturated at lower oxygen pressures than haemoglobin. The latter is also present, often in muscles, especially the fast-working muscles of the buccal mass.

Excretion

The kidney is a coelomoduct with deeply folded walls, and is usually linked to the pericardial cavity by a renopericardial canal. It opens to the mantle cavity either directly or by way of a nephridioduct (Fig. 14.15B, C). In the vetigastropods, the left renal organ is smaller than the functional right one, through which the gametes pass. In all other gastropods, there is a single auricle, the left renal organ is the functional kidney, and separate gonoducts have evolved. In many opisthobranchs, the external opening of the kidney is situated near the anus and at the base of the gill (Fig. 14.17A). In most pulmonates, the kidney discharges into the pulmonary cavity by a papilla, or a long ureter is present which opens beside the anus (Fig. 14.19B).

The initial stage of urine production by gastropods, pulmonates excepted, appears to involve ultrafiltration from the heart into the pericardial cavity, and then into the kidney by way of the renopericardial duct (Martin 1983; Andrews 1988). The pericardial epithelium is sometimes thickened, to form deep brown pericardial glands which lie over the auricle wall, and these glands are involved in the filtration process. In the terrestrial pulmonates, the pericardium does not function in the filtration of urine. Excretory fluid filters directly from the renal capillaries into the kidney (Vorwohl 1961, cited in Fretter 1975).

The arrangement of kidney and ureter in the Stylommatophora – the terrestrial pulmonates – has significant functional and evolutionary implications. The ordinal division into the Orthurethra (Achatinellidae, Cionellidae, Vallonidae, Pupillidae, Pleurodiscidae and Enidae in Australia; Smith 1992), Mesurethra and Sigmurethra (most Australian land snails), as their names imply, is based on the arrangement of the kidney and ureter. In the Orthurethra, the long, straight ureter opens near the pneumostome. The ureter in the Mesurethra is short and opens near the side of the kidney, and in the Sigmurethra, it follows the intestine anteriorly to the mantle edge.

As a functional consequence of the orthurethran and mesurethran conditions, the excretory products are released into the pulmonary cavity and must subsequently be flushed out. A water reserve of from a few drops to one-twelfth the body weight of the snail present in the pallial space of these snails serves the purpose (Solem 1974a). A significant step in the evolution of the pulmonary cavity, therefore, was the formation of a water-resorbing ureter

14. CLASS GASTROPODA

which opens externally by way of the pneumostome. The long, externally opening ureter in the Sigmurethra and its role in water conservation paved the way for the evolution in the Stylommatophora of the shell-less, slug habit, found only in this order (Runham & Hunter 1970; Solem 1978).

FEEDING AND DIGESTION

Buccal Mass and Radula

The radula, a structure unique to molluscs, is the principal food-collecting organ in gastropods. It is a tooth-bearing ribbon borne on a muscular bulb, the odontophore, which is manipulated by a complex array of muscles. The entire structure—radula, odontophore and muscles—is termed the buccal mass (Figs 14.14, 14.21). Modifications of the radular/buccal complex and concomitant changes in the gut are the basis for much of the adaptive radiation in gastropods, in which virtually every conceivable source of food on land and in the sea has been exploited, as herbivores, deposit-feeders, suspension-feeders, scavengers, parasites and predators. In exploiting these food resources, gastropods scrape, browse, bore, suck fluids from algal cells, crush, tear, and impale their food. Recent reviews of gastropod feeding biology and the digestive system include those of Owen (1966a, 1966b), Purchon (1968), Runham (1975), Kohn (1983), Salwini-Plawen (1988) and Fretter & Graham (1994).

Six different radular types are usually identified among 'prosobranchs' (see Fig. 1.14). The rhipidoglossate radula (see Fig. 1.14B) has one or more large central or rachidian teeth and large numbers of lateral and marginal teeth. It is found in all

vetigastropods (for example, fissurellids and trochids) and in the neritoidaeans. Patellid limpets (Patellogastropoda) have a docoglossate radula (see Fig. 1.14A), with two or three strong, robust and often mineralised lateral teeth in each row, and usually some other teeth (see also Fig. 15.34). Many caenogastropods have a taenioglossate radula (Fig. 1.14C) in which there are seven teeth in each row, each tooth with denticles and cusps. The ptenoglossate radula, as found in the Epitoniidae and Janthinidae, has many similar, usually fang-like teeth. There are only three teeth in each row of the rachiglossate radula of muricid and buccinid neogastropods (see Fig. 1.14D). A second radular type found in neogastropods, the toxoglossate radula, consists of long slender marginals as in turrids or single pairs of hollow, barbed teeth (see Fig. 1.14E) which are filled with poison. Rhachiglossate and toxoglossate taxa have been grouped together as the Stenoglossa, with reference to the narrow radula, though they are dissimilar in other respects (Cox 1960b).

Many primitive opisthobranchs and pulmonates have a broad radula and numerous teeth (Morton 1955b). The radula in the anaspidean opisthobranch genus *Aplysia* bear very uniform teeth. Several tooth types occur in more specialised opisthobranchs such as pleurobranchs and dorids (see Figs 16.10C, 16.75–16.83). In doridoideans, radular morphology appears to be closely associated with food type (Young 1969a). For example, dorids that eat bryozoans typically lack a central tooth, and have one very large lateral and seven to 15 small marginal teeth on each side (Nybakken & McDonald 1981). Opisthobranchs show an overall tendency towards reduction in the number of radular teeth. Aeolids have as few as three distinctively differentiated teeth in each radular row (see Fig. 16.103C–E), and in sacoglossans there is a single tooth in each row.

The pulmonate radula is typically composed of a large number of very small teeth—as many as 250 000 in snails that feed on the juices of fungal hyphae (Solem 1974a). Pulmonate radula teeth were long thought to be quite simple, but scanning electron microscopy shows considerable tooth specialisation and complexity (see Fig. 17.10). For example, striking differences in tooth form and support mechanisms occur in two desert camaenid pulmonate snails from Cape Range, Western Australia, which may specialise on different food plants (Solem 1974b). Carnivorous land snails tend to have fewer teeth than do herbivores and the cusps are elongate (see Fig. 17.10B; Solem 1973).

Radula Form and Function

Only recently have the complexities of radula tooth structure and function been described and understood. The traditional picture of a radula is of a flat ribbon of teeth. Using scanning electron microscopy, Runham (1969) could describe the change in position of radular teeth from the flattened resting position into an erect position as they pass over the odontophore (Fig. 14.22A); indeed, in the conventional orientation for illustrating radulae, tooth cusps have been shown down and in reverse orientation from the way they appear in the feeding position (Hickman 1980). In their description of radular configuration in a feeding turban snail, *Tegula funebris*, Morris & Hickman (1981) showed that the rows of radular teeth actually form a tight semicircle. They proposed a 'slit cylinder model' of the odontophore, in which the 'radula is depicted as a slit cylinder posteriorly and a flat band anteriorly, with a movable semicircular crease at the region of transition where contact is made with the substratum' (Fig. 14.22B). The orientation of teeth in enrolled and elevated radulae may be compared in the micrographs in Figure 14.22C, D.

In flat view, radula teeth consist of a base, shaft and cusp. The tooth base may interlock with the base of the tooth immediately in front, transmitting pressure from the cutting edge of the tooth in one row to the basal plate of the tooth immediately in front of it (Solem 1972a). The shaft of one tooth may interlock with the shaft of another tooth and distribute and transfer stress (Solem 1972a; Hickman 1980).

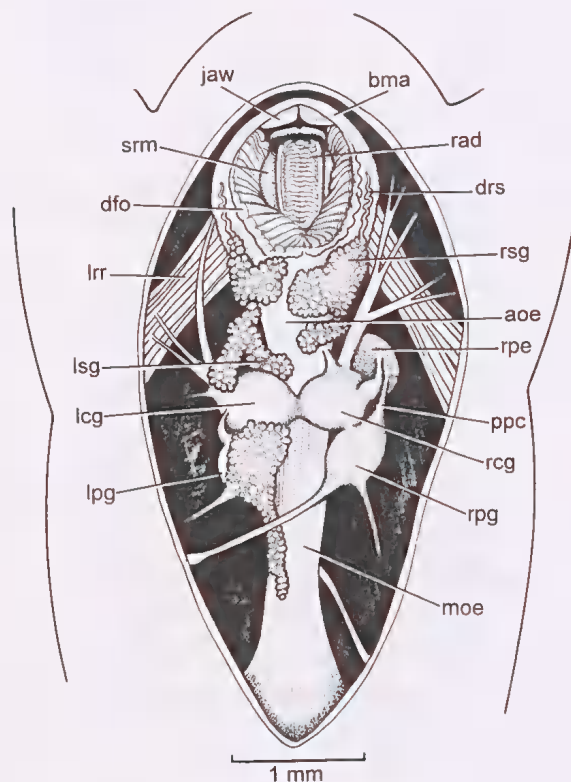


Figure 14.21 The buccal cavity, opened mid-dorsally, and the anterior alimentary canal, viewed dorsally, of the caenogastropod *Modulus modiolus* (Modulidae), showing the arrangement of salivary glands, nerve ring and mid-oesophagus. aoe, anterior oesophagus; bma, buccal mass; dfo, dorsal fold of oesophagus; drs, duct of right salivary gland; jaw, jaw; lcg, left cerebral ganglion; lpg, left pleural ganglion; lrr, left radular retractor muscle; lsg, left salivary gland; moe, mid-oesophagus; ppc, pleural-pedal connective; rad, radula; rcg, right cerebral ganglion; rpe, right pedal ganglion; rpg, right pleural ganglion; rsg, right salivary gland; srm, subradular membrane. (After Houbriek 1980) [M. Thompson]

From studies of the rhipidoglossate radula, Hickman (1980) divided the radula (Fig. 1.14A) into three major fields – the food-preparation area, the food-gathering teeth, and a central field of robust rachidian and lateral teeth, with two fields of finer marginal teeth on each side. Such radulae function as gathering tools. The radular teeth of the docoglossate radula of patellids interact with the substratum like a rasp (Fig. 1.14B) (Lindberg 1988). This action is the result of the radula moving over the flat bending plane of the odontophore and therefore does not splay laterally – the stereoglossate condition (Salvini-Plawen 1988). The curved bending plane of the odontophore in other gastropods splays the marginal teeth as the radula moves forward – the flexoglossate condition. These teeth act like a broom while the lateral and central teeth remove food in the form of particles or small chunks from the substratum. Caenogastropods that graze on soft corals, sea anemones, colonial ascidians and bryozoans presumably utilise the radula in a similar manner. Examples are *Lamellaria*, *Trivia* as well as ovulids, and aeolid and dorid opisthobranchs. Browsers use rhythmic radular and jaw movements to ingest large, irregularly shaped pieces of food, as

described for *Aplysia* (Jahan-Parwar & Fredman 1983). Species of the rhytidid pulmonate genus *Ptychorhytida*, which feed on earthworms, use the teeth to stab and tear their food. In the voracious tropical carnivore *Euglandina rosea*, the teeth are blade-like slicers (Solem 1974a).

Fluid-Feeders

Slugs of the opisthobranch order Sacoglossa are specialised as feeders on the cell contents of green algae. The radula is peculiarly fashioned, lying in a tapering tube which opens through the floor of the pharynx. Only one tooth is in use at a time. Sacoglossans are highly specific in their food plants and their tiny, pointed, blade-like teeth are adapted to the cell size of the species concerned (Jensen 1980, 1983, 1991).

Predation

Predators search, pursue, capture, immobilise and consume their prey in a complex sequence of behaviours. Structural adaptations in caenogastropod predators (Fig. 14.23) include: a well-developed siphon and chemosensory osphradium that locate the prey; an often highly extensible proboscis which carries the odontophore to otherwise inaccessible sites, and which may also envelop the prey; radula teeth modified for tearing, scraping, drilling or impaling the prey; glands that secrete toxins that immobilise the prey; glands in the foot or proboscis that aid in the dissolution of shelled prey (Ponder 1973; Taylor, Morris & Taylor 1980). Pulmonate predators also have adaptations, including sharp teeth, a short proboscis and lack of a siphon. *Euglandina rosea*, from Florida, has a well-developed proboscis (Cook 1985), and the everted mouthparts are brought down rapidly onto the prey; a successful strike results in penetration by the radular teeth. The teeth of the European terrestrial slug genus *Testacella*, which has been introduced to Australia, act as harpoons (Solem 1974b).

There are as many ways of feeding as there are kinds of prey. Some carnivorous gastropods swallow their prey whole, as do the large tonnids that envelop holothurians in the highly extensible proboscis (Fig. 14.23B; Hughes & Hughes 1981), and aglajid opisthobranchs that engulf shelled gastropods and worms (Rudman 1972b). The sand-dwelling opisthobranch *Philine aperta* everts its buccal mass and grabs its small bivalve prey with the radular teeth; the shells are crushed in its oesophageal gizzard (Hurst 1965). In members of the pulmonate family Rhytididae, the buccal mass is elongated and greatly enlarged (Solem 1974a), and large prey such as snails and earthworms can be drawn into it using the elongate recurved radular teeth (Smith 1971).

Members of the families Capulidae (Kabat 1990), Cassidae, Naticidae, Muricidae, some Marginellidae (Ponder & Taylor 1992), one opisthobranch family, the Vayssiéridae (Young 1969b), and some members of the pulmonate family Zonitidae (Mordan 1977) drill and then feed on their prey. Cassids feed almost exclusively on echinoids (Fig. 14.23F). They hold down even such spiny forms as *Diadema* species with the large foot and drill a hole through the test with the proboscis which is then inserted (Hughes & Hughes 1981). Cassids use sulphuric acid from the probosceal gland together with the radula to penetrate the echinoid test. Naticids and muricids also use acids and chelating agents secreted by probosceal glands and pedal glands, respectively, in combination with mechanical scraping by the radula, to drill through the shells of their molluscan prey. The fluid contents of the prey are drawn up through neat, circular holes (Hyman 1967). The minute dorid opisthobranch, *Okadaia elegans* (Vayssiéridae), of the Pacific Ocean, no more than 5 mm in length, uses radular action to drill small round holes in the shells of spirorbicid worms (Young 1969b).

Toxoglossate gastropods immobilise a large prey item with a 'chemically aided rapid-strike' mechanism (Shimek & Kohn 1981) before it is swallowed whole (Fig. 14.23A). The usual prey are annelids, but enteropneusts, echinurans, sipunculans, fishes and other gastropods are also captured. The cone shells are among the

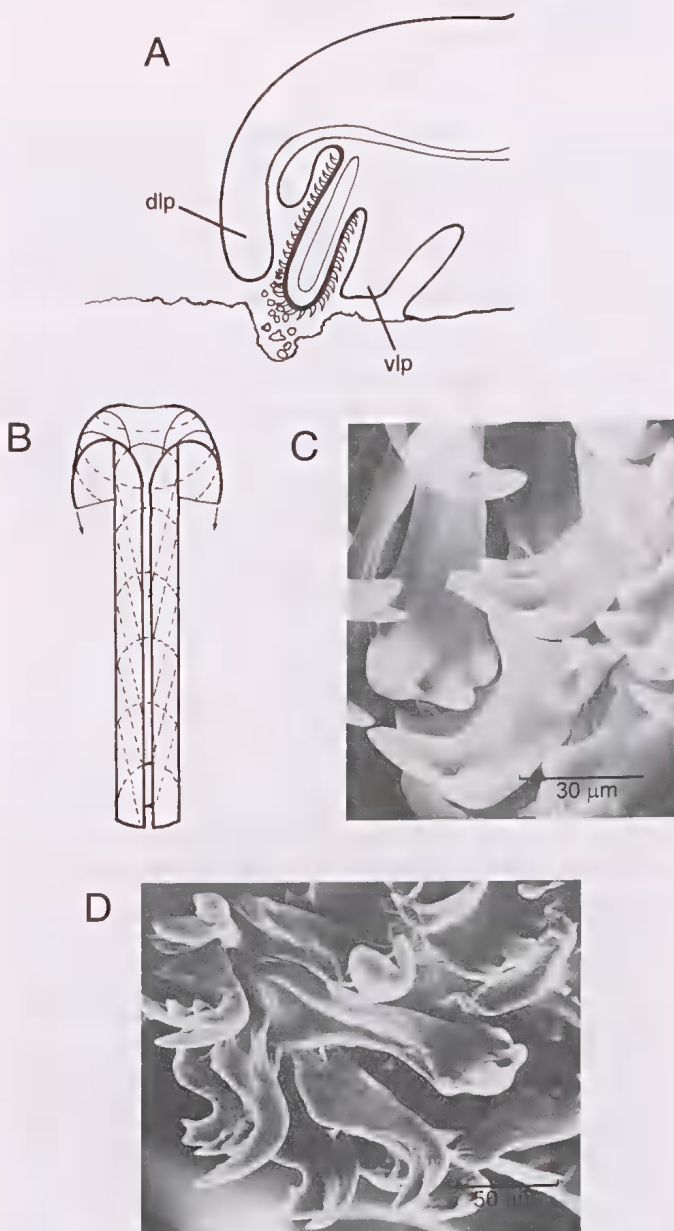


Figure 14.22 Radula function. A, mid-sagittal section with the radula shown as a flat, toothed ribbon that moves over a 'bending plane'. B, model of a radula as a slit cylinder posteriorly and a flat band anteriorly. C, D, radular teeth of a terrestrial prosobranch, *Ostodes* sp. (Poteriidae), from Western Samoa: C, enrolled central and right lateral teeth; D, central and marginal teeth in the elevated position. dlp, dorsal lip; vlp, ventral lip. (A, B, after Hickman 1985b; C, D, after Solem 1974a) [A, B, M. Thompson]

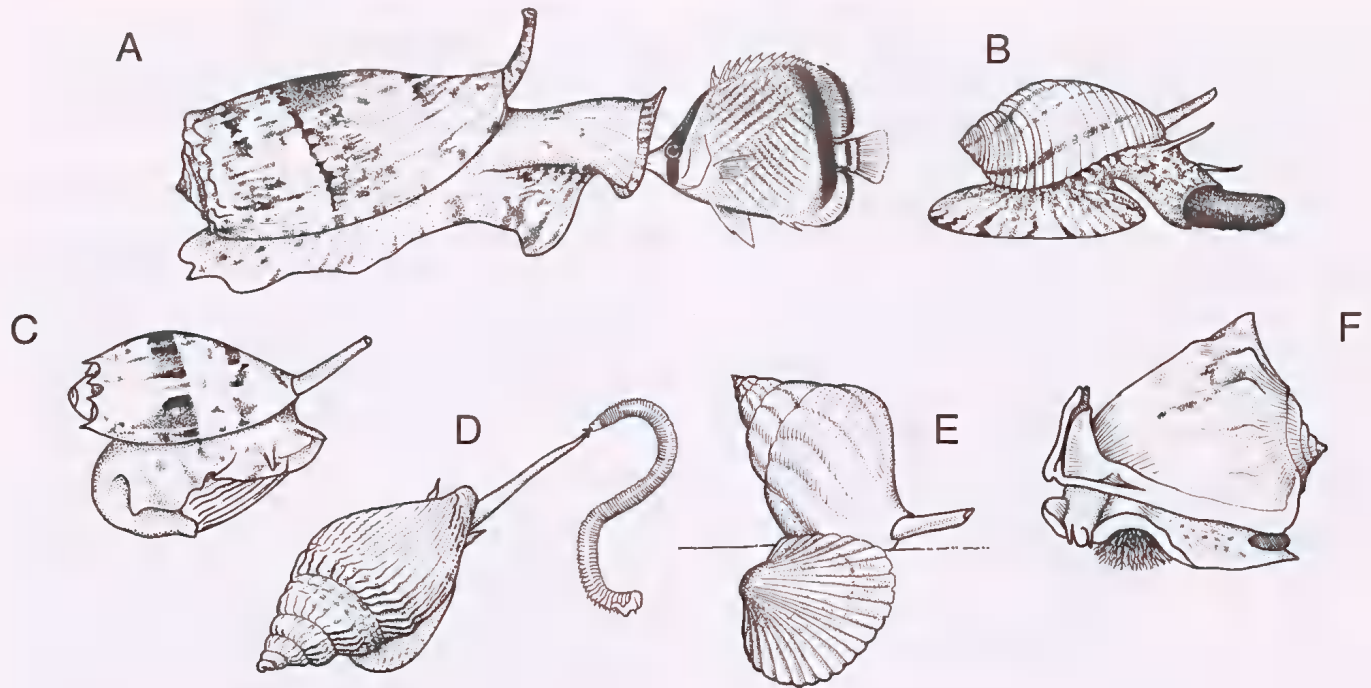


Figure 14.23 Some predatory caenogastropods attacking their prey. **A**, *Conus geographus* (Conidae) enveloping a small chaetodontid fish. **B**, *Tonna perdx* (Tonnidae) feeding on a holothurian. **C**, *Melo amphora* (Volutidae) enveloping another volute *Amorja zebra*. **D**, *Lora trevelliana* (Turridae) impaling a polychaete. **E**, *Buccinum undatum* (Buccinidae) wedging open a cockle. **F**, *Cassis tuberosa* (Cassidae) feeding on an echinoid. (After Taylor 1981) [M. Thompson]

most studied of gastropod predators (Kohn 1959; Shimek & Kohn 1981). They inject a neurotoxin into their prey using the harpoon-like radula teeth. There is no odontophore, but the radular caecum contains a sheaf of slender, barbed teeth (see Fig. 1.14E). The shaft forms a partly closed tube, which conveys the poison from the poison gland, a modified oesophageal gland.

Predatory gastropods eat a wide variety of prey and some families include species with catholic diets. The European buccinid, *Buccinum undatum*, for example, feeds on species from seven or eight different phyla (Taylor 1981). The carnivorous pulmonate *Euglandina rosea* feeds on an array of other terrestrial gastropods, and possibly on freshwater snails as well. Other predators are highly specialised in their diets. Terrestrial slugs, *Testacella* species, specialise on earthworms (Solem 1974b). All species of the Mitridae so far examined have been found to feed on sipunculid worms (Kohn 1970). The gymnosomatous pteropod *Clione limacina* feeds only on species of *Spiratella*, a genus of thecosomatous pteropod (Lalli 1970). Dorid nudibranchs are usually specific to single species of sponge (Young 1969a); Rudman (1981a, 1981b, 1981c) commented on the specificity of aeolids on hydroids, sea anemones, opisthobranch egg masses, alcyonarians, and scleractinian corals.

Feeding without a Radula

Although the radula is often considered an essential component of gastropod feeding, some gastropods have no radula. Several members of the neogastropod family Terebridae which lack a radula and venom apparatus use the tubular rhynchodaeum to engulf prey such as enteropneusts and polychaetes (Miller 1975). The nudibranch *Melibe leonina* lacks both radula and buccal mass and feeds by casting a cephalic veil, like a net, over small crustaceans (Hurst 1968). In another American west coast opisthobranch, *Navanax inermis*, a voracious predator of opisthobranchs, the intrinsic muscles of the buccal mass or pharynx are embedded in a matrix of connective tissue and form an expandable tube between the mouth and oesophagus. Prey is ingested by suction created by the expansion and eversion of the pharynx (Woollacott 1974). Though less active than the predators described above, the coral-dwelling Muricidae also lack a radula, and use the buccal cavity as a pump in feeding on cnidarian prey (Ward 1965).

Most eulimoidean parasites lack a radula. For example, the limpet-like eulimids of the genus *Thyca* parasitise starfish; they lack both radula and jaws, and suck coelomic fluid through the integument of the host using a long proboscis. Other eulimoideans may lack buccal mass, radula, jaws and salivary glands. The specialised ectoderm parasites of diadematid echinoids feed through the proboscis which leads to a buccal cavity that functions as a pump. The tip of the short proboscis of *Pulicicochlea calamaris* forms a suction cup that grasps the epidermis of the host's spine and pulls on it, detaching pieces that are then swallowed (Ponder & Gooding 1978). Another species inserts its long proboscis into the body cavity of the host. Endoparasites such as species of *Stilifer* also lack a radula.

Suspension-feeding

Suspension-feeding on food particles in the water column involves modifications of the mantle cavity and other structures as well as the radula. This feeding mode has arisen independently in at least seven marine families—the sedentary Capulidae, Calyptraeidae and Vermetidae, and the free-living Turritellidae, Struthiolariidae, Trochidae and Neomphalidae—and in some freshwater caenogastropods and the thecosomatous pteropods.

In sedentary caenogastropods like vermetids, the shape of the gill filaments and ciliary currents in the mantle cavity, the size of the pedal gland relative to the foot, and the proportions of the buccal mass and the head are associated with the type of feeding habit. *Dendropoma maxima* from the Great Barrier Reef (Fig. 14.24A) is a ciliary feeder (Yonge 1938). In this species a strong inhalant current flows through the left side of the mantle cavity, and the large, elongate gill filaments carry copious amounts of mucus secreted by the hypobranchial gland. Food particles, bound up in the mucus, are moved in ciliated food grooves toward the mouth, and the radula draws the mucous string to the mouth. Several vermetids in the genera *Dendropoma* and *Serpulorbis* (in part) (Hadfield, Kay, Gillette & Lloyd 1972) cast out webs of mucous threads in which water-borne particles are captured. In these gastropods the pedal gland, which is the source of the mucus, is large relative to the size of the foot and the buccal mass is small relative to the size of the head. Ciliary and mucous thread feeding are not mutually exclusive, and both types of feeding may occur simultaneously (Morton 1965; Hadfield *et al.* 1972).

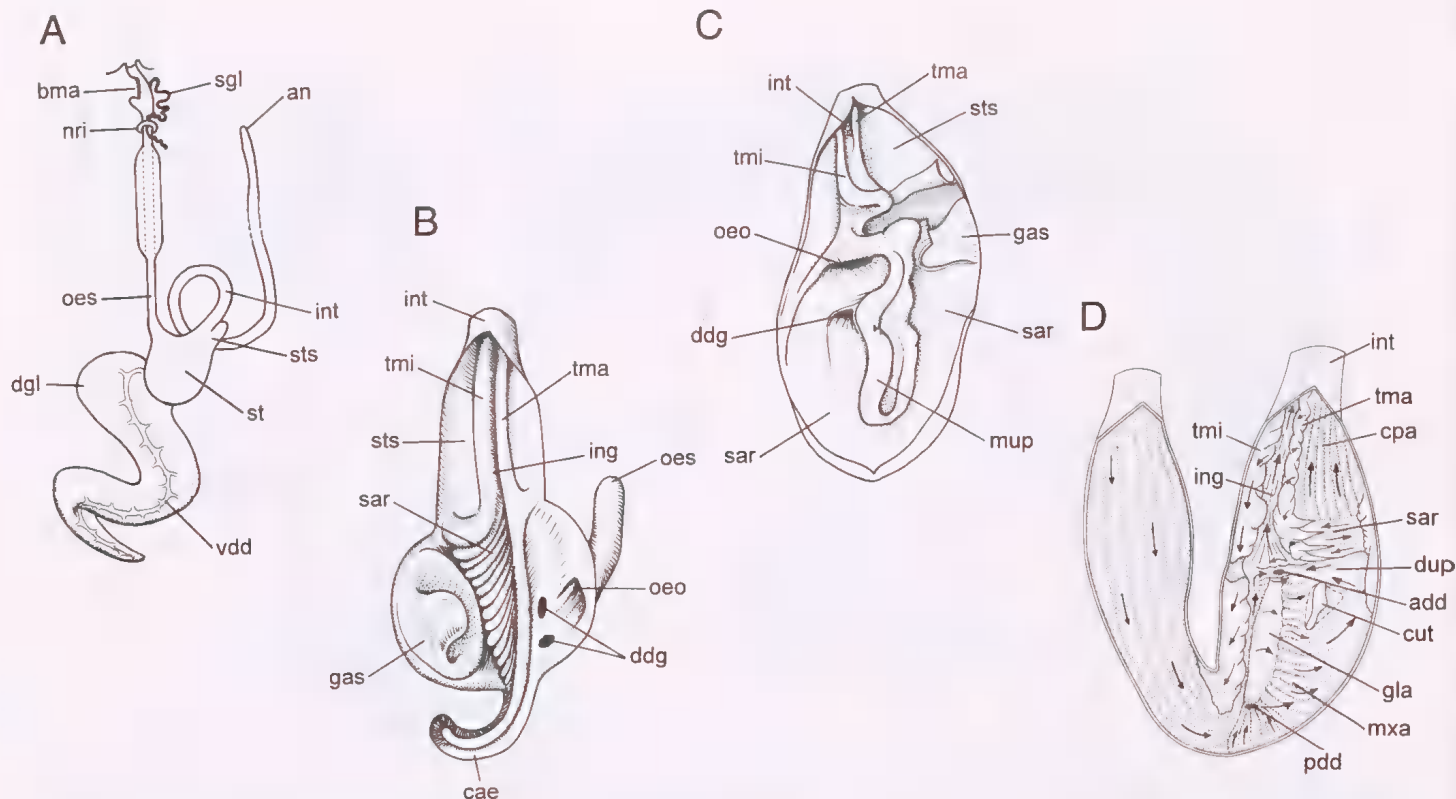


Figure 14.25 The structure of the caenogastropod alimentary tract. **A**, gut of the cerithioidean *Clypeomorus bifasciata* (Cerithiidae). **B**, a generalised caenogastropod stomach, showing the richly ciliated sorting area, typhlosoles extending into the caecum, the cuticle forming the gastric shield against which the protostyle is rotated, and the style sac which opens into the intestine. **C**, the simplified stomach of the caenogastropod *Planaxis sulcatus* (Planaxidae). **D**, the U-shaped stomach of the neogastropod *Colus gracilis* (Buccinidae). an, anus; add, anterior duct of digestive diverticula; bma, buccal mass; cae, caecum; cpa, compacting area; cut, cuticularised area; ddg, ducts of digestive gland; dgl, digestive gland; dup, duct pouch; gas, gastric shield; gla, glandular area; ing, intestinal groove; int, intestine; mup, raised muscular pad; mxa, mixing area; nri, nerve ring; oeo, oesophageal opening; oes, oesophagus; pdd, posterior duct of digestive diverticula; sar, sorting area; sgl, salivary glands; st, stomach; sts, style sac; tma, major typhlosole; tmi, minor typhlosole; vdd, ventral duct of digestive gland. (A, after Houbbrick 1985; B, after Fretter & Graham 1962; C, after Houbbrick 1987; D, after Smith, E.H. 1967) [M. Thompson]

oesophagus and intestine. Fretter (1939) described the stomach of a shelled cephalaspid, genus *Acteon*, which has no gizzard and retains some features of the primitive gastropod stomach. There is an elaborate gizzard in another shelled cephalaspid genus, *Haminoea* (Fig. 14.26B), and thin-walled stomachs in carnivorous opisthobranch genera, such as *Philine* and *Scaphander*, which are almost completely embedded in digestive gland. The anterior oesophagus, crop and gizzard can be highly dilated in *Philine* and *Scaphander*. In primitive pulmonates, such as ellobiids, the structural plan of the stomach resembles that of primitive gastropods (Fig. 14.27B) with a ciliated sorting area, and cuticular area centred on the gastric shield and caecum. In other pulmonates, the familiar landmarks of the gastropod stomach have disappeared and the stomach and oesophagus have become muscular triturating organs. The stylommatophoran stomach (Fig. 14.27C) is both reduced and specialised; the posterior oesophagus is dilated as a muscular crop in which food is digested and the stomach no longer receives and breaks down food. In basommatophorans, such as *Lymnaea*, powerful muscular lobes in the anterior portion of the stomach function as a gizzard (Fig. 14.27E).

Digestion

In most gastropods, digestion is both extracellular and intracellular. This process was reviewed recently by Voltzow (1994). The digestive gland is the largest organ in the gastropod body, perhaps because of the complexity of the digestive process (Fig. 14.14). It is a large brown structure built up of small follicles and ramifying ducts. Among its functions are the secretion of enzymes, the absorption of food materials, the storage of reserve materials, and excretion. It accumulates indigestible material as yellow granules which are then conveyed by cilia to the stomach. Cells which function as calcium stores may be present.

Among the enzymes secreted by the digestive gland are lipases, proteases and carbohydrases. Some of these may be secreted into the stomach where digestion takes place. From the stomach, nutrient material enters the ducts of the gland and final intracellular digestion takes place in phagocytic cells in the gland. The relative importance of extracellular and intracellular digestion is closely related to the method of feeding. Herbivorous caenogastropods that feed continuously depend on intracellular digestion, whereas extracellular digestion predominates in gastropods that feed intermittently (Fretter & Graham 1962).

In addition to the digestive gland, several other glands associated with digestion may be present. Even in the most primitive gastropods, glands in the anterior oesophagus secrete both mucus and extracellular enzymes such as amylase and cellulase (Graham 1932). These glands become more complex in predatory caenogastropods. In *Cassis*, a secretion rich in sulphuric acid (pH < 1) is provided by glands in the proboscis (Hughes & Hughes 1981). The salivary glands of cymatiids and bursids (Houbbrick & Fretter 1969) produce toxins that have marked anaesthetic effects on their prey. The poison gland of *Conus* and other conoideans is the homologue of the oesophageal gland of other gastropods (Ponder 1973).

REPRODUCTION

In view of the diversity of gastropods it is hardly surprising that the reproductive morphologies and strategies of the various groups are equally diverse. Because of space limitations and the availability of several detailed reviews of reproduction in various groups, this section is brief. Readers are referred to the relevant chapters in this work for each group and to the following sources for further information on prosobranchs – Webber (1977), Fretter (1984), Hickman (1992); opisthobranchs – Beeman (1977), Hadfield & Switzer-Dunlap (1984); and pulmonates – Duncan (1975), Berry (1977), Geraerts & Joosse (1984) and Tompa (1984).

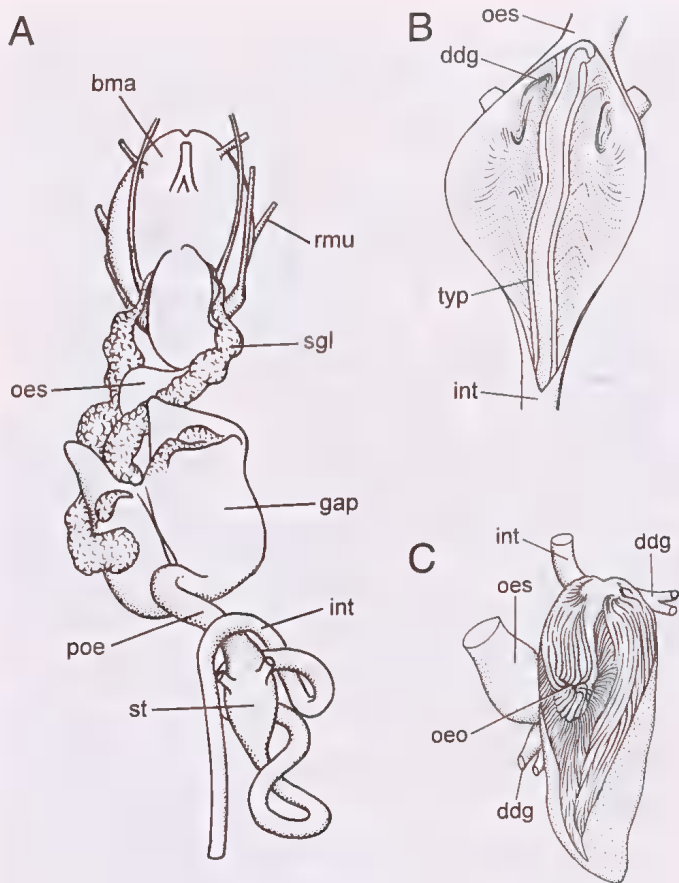


Figure 14.26 The opisthobranch alimentary canal. A, the alimentary canal of the herbivorous cephalaspid *Haminoea zelandiae* (Haminoeidae). B, the stomach of *Haminoea zelandiae*. C, the stomach of the carnivorous cephalaspid *Hydatina physis* (Hydatinidae). bma, buccal mass; ddg, ducts of digestive gland; gap, gastric pouch; int, intestine; oeo, oesophageal opening; oes, oesophagus; poe, posterior oesophagus; rmu, radular muscle; sgl, salivary gland; st, stomach; typ, typhlosome. (A, B, after Rudman 1971a; C, after Rudman 1972a) [M. Thompson]

Reproductive Morphology

Sexes are separate in most prosobranchs and the single gonad in the upper whorls is closely associated with the digestive gland (Figs 14.1, 14.15). Reproductive morphology is simplest in the prosobranchs and Heterostropha, and more complex in opisthobranchs and pulmonates.

In patellogastropods and vetigastropods, the reproductive system is simple (Fig. 14.28A, B) and is usually similar in males and females. It consists of a single gonad with a gonoduct leading to the functional right kidney. Gametes are released into the kidney and escape through the kidney pore into the surrounding water. Fertilisation is external and, in most species, gametes are simply shed into the water column with a protective covering for the eggs, but no egg mass is formed. In some other species, a glandular region in the distal portion of the right kidney duct produces mucus which binds the eggs together in a mass.

In caenogastropods, reproductive morphology is more complex. The gonoduct is separated from the functional right kidney and opens directly into the mantle cavity. The male and female reproductive systems differ in their morphology. In the basic male system (Fig. 14.28C) a gonoduct extends from the testis to the prostate gland. The open or closed pallial vas deferens then leads towards the penis which, when present, is typically located on the right side of the neck.

The more complex female reproductive system has more functions than that of the male. The oviduct extends from the ovary to the mantle cavity and is composed of at least two glandular areas. The posterior albumen and anterior capsule

glands (Fig. 14.28D) encase the egg and elaborate the egg case. A pedal gland on the foot of neogastropods moulds the egg capsules and attaches them to the substratum in species in which attachment occurs. Specialised areas of the female gonoduct receive sperm during copulation (the bursa copulatrix) and subsequent sperm storage (seminal receptacle).

Sperm are transferred from the male to the female during copulation. Copulation may last from a few minutes to many hours, during which the two individuals are in close contact, with the male above the female and on her right (Fig. 14.29). A penis is absent in some groups of caenogastropods and there are alternative mechanisms of sperm transfer, including the use of spermatophores (reviewed by Robertson 1989).

Few caenogastropods are known to be simultaneous hermaphrodites, but species of several groups, for example, the Epitoniidae, Janthinidae, Capulidae, Calyptraeidae and Hipponicidae, undergo sex reversals. Australian species in which sex reversal is known to occur include *Crepidula aculeata* and

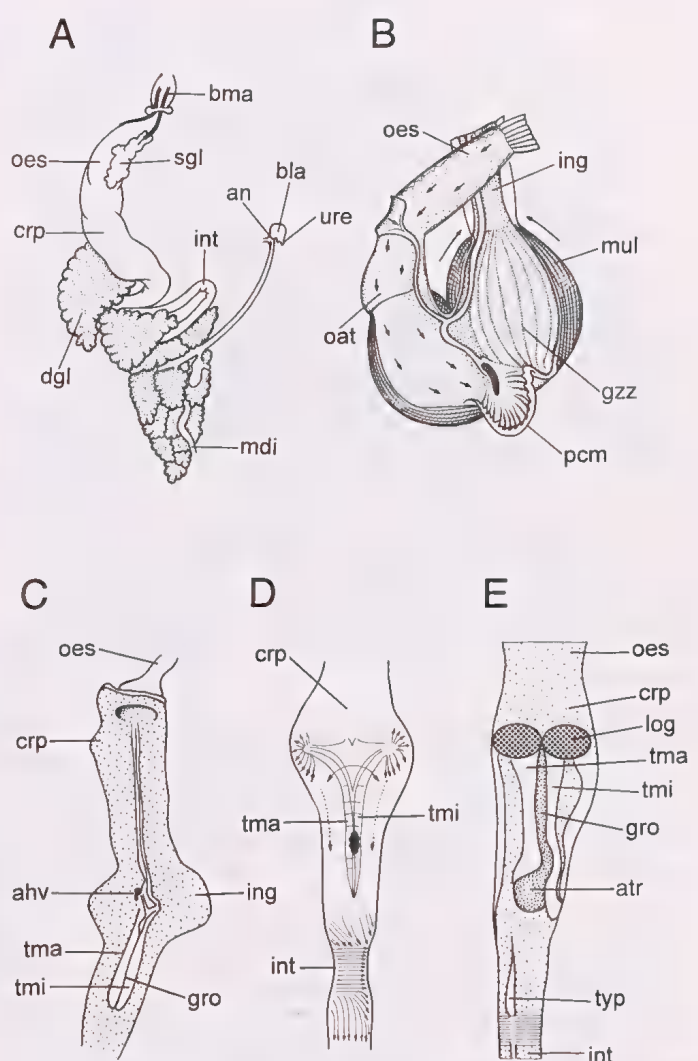


Figure 14.27 Structure of the pulmonate alimentary tract. A, the regions of the alimentary canal and accessory glands of *Deroceras reticulatum* (Limacidae). B, the stomach of the advanced ellobiid genus *Ophicardelus*, showing muscular walls. C, crop and stomach of the stylommatophoran *Oxychilus* (Zonitidae). D, stomach of the stylommatophoran slug *Ariolimax* (Arionidae). E, stomach of the basommatophoran *Lymnaea* (Lymnaeidae). ahv, anterior hepatic vestibule aperture; an, anus; atr, atrium; bla, bladder; bma, buccal mass; crp, crop; dgl, digestive gland; ddg, duct of digestive gland; gro, groove; gzz, intestinal portion of gizzard; ing, intestinal groove; int, intestine; log, lobe of gizzard; mdi, mid-intestine; mul, muscle layer of gizzard wall; oat, oesophageal atrium; oes, oesophagus; pcm, posterior caecum; rmu, radular muscles; sgl, salivary glands; st, stomach; typ, typhlosome; tma, major typhlosome; tmi, minor typhlosome; ure, ureter. (A, D, after Walker 1972; B, after Morton 1955b; C, after Rigby 1963; E, after Carriker 1946) [M. Thompson]

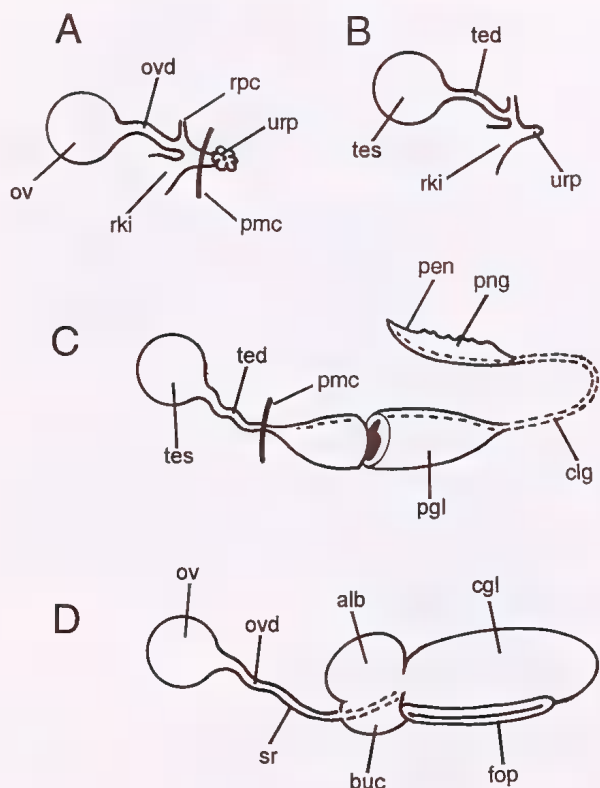


Figure 14.28 The reproductive system of representative prosobranch gastropods. A, B, Vetigastropoda. C, D, Caenogastropoda. A, female *Gibbula* and *Monodonta* (Trochidae). B, male *Calliostoma* (Trochidae). C, male *Littorina littorea* (Littorinidae). D, female *Pomatias elegans* (Pomatiasidae). alb, albumen gland; buc, bursa copulatrix; cgl, capsule gland; clg, ciliated groove; fop, female opening; ov, ovary; ovd, oviduct; pen, penis; pgl, prostate gland; pmc, posterior limit of mantle cavity; png, penial gland; rki, right kidney; rpc, renopericardial duct; sr, seminal receptacle; ted, testicular duct; tes, testis; urp, urinogenital papilla. (After Fretter & Graham 1962) [M. Thompson]

Janthina janthina. The population of *Hipponix australis* at Albany, Western Australia, exhibits protandrous hermaphroditism (Knudsen 1991). A few freshwater prosobranchs have been reported to be parthenogenetic, including members of the genus *Thiara* in Australia (Stoddart 1985) and the introduced hydrobiid *Potamopyrgus antipodarum*.

In opisthobranchs, the reproductive system is much more complex and variable than it is in caenogastropods. All opisthobranchs are hermaphroditic. Some, such as the gymnosomes and thecosomes are protandrous, developing first into functional males, then continuing into a functional female stage. Most others are simultaneous hermaphrodites.

Opisthobranchs are morphologically diverse, particularly in their reproductive systems. There is no 'typical' opisthobranch reproductive system, but the reproductive morphology of aplysiids, a group of intermediate complexity, has been described in detail by Beeman (1977), whose work should be consulted for information on variations encountered in the different opisthobranch orders. The present account relies heavily on Beeman's (1977) comprehensive description, and further details are presented in Chapter 6 in this volume. As far as possible, the same terminology has been applied here to organs of similar functions in opisthobranchs as has been used for caenogastropods, and the same procedure is followed later for the pulmonates.

Hermaphroditism is regarded by both Ghiselin (1966b) and Webber (1977) as an evolutionary adaptation to situations in which the likelihood of finding a mate is low. Once a partner is found, each individual can function as either sex, thereby effectively doubling the chances of successful copulation. Sperm received during mating are simply stored until they are required for the fertilisation of mature ova.

Opisthobranchs have a single gonad, the ovotestis. In the primitive condition a single gonoduct leads to the external environment. Aside from the fact that the gonad is hermaphroditic, this basic arrangement does not differ greatly from that of caenogastropods, and the functions occurring in the two sexes in caenogastropods are all accomplished in one individual in opisthobranchs. The major modification lies in the elaboration of a series of complex glands and chambers along the course of the gonoduct. This elaboration can be divided into male and female components.

In the female portion of the reproductive system (Fig. 14.30) ova are transported through the coelomic gonoduct to the fertilisation chamber. In the remainder of the gonoduct, termed the pallial gonoduct, the glands are associated with the female system. First encountered is the albumen gland which provides nutritive material used by the fertilised egg as it develops. The egg and its albumen are enclosed in a membrane by the membrane gland, then coated in mucus by the mucous gland, and finally transported to the external environment through the common genital pore. The atrium, which contains an atrial gland of uncertain function, grasps the penis during copulation. Exogenous sperm (that produced by another individual) received during copulation move to the bursa copulatrix and subsequently accumulate in the seminal receptacle. Endogenous sperm produced in the ovotestis are found in a widened area of the coelomic gonoduct known as the ampulla. During copulation, these sperm move along the ciliated genital groove to the penis at the right side of the head. The groove is external in primitive forms such as anaspideans and cephalaspideans but forms a closed tube, the vas deferens, in more advanced forms. A prostate gland is often present, located at the base of the penis.

The basic system described above, in which there is a single, undivided pallial gonoduct, is termed monaulic, referring to the single tube present. In more complex opisthobranch reproductive systems, the gonoduct may be differentiated into two (diaulic) or even three (triaulic) separate tubes. In the triaulic system, the most complex, a vas deferens which transports endogenous sperm, a vaginal duct in which the exogenous sperm are found, and a separate oviduct through which oocytes and zygotes move are all present.

Copulation is reciprocal in most opisthobranchs; the right side of the head is held in close contact with that of another while they face each other (Fig. 14.31A). In some taxa, notably anaspideans, one individual mounts another from behind and acts as a male (Fig. 14.31B). Aplysiids are well known for forming mating groups of perhaps a dozen individuals in which each individual acts as a male to the individual in front of it and a female to the one behind. The mating individuals can form a complete circle. Spermatophores are known in 15 opisthobranch species in five different orders (Robertson 1989), including a number of thecosome species which occur in Australia (Lalli & Wells 1978; Lalli & Gilmer 1989).

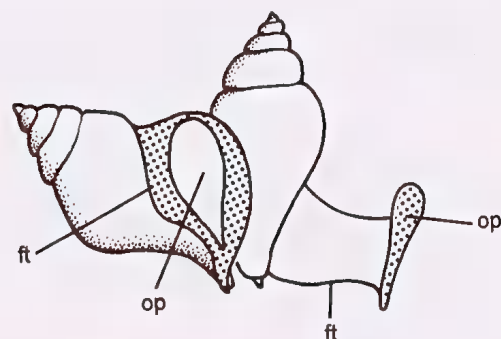


Figure 14.29 Copulatory position of *Fasciolaria* sp. (Fasciariidae). The male is on the left. ft, foot; op, operculum. (After Wells 1970)

[M. Thompson]

Pulmonates, like opisthobranchs, are hermaphroditic. The more primitive forms may be protandrous. The majority, however, are simultaneous hermaphrodites, and in most there are mechanisms that prevent self-fertilisation. Some stylommatophorans are parthenogenetic.

Reproduction in pulmonates has been reviewed recently by Duncan (1975; pulmonates), Berry (1977; marine pulmonates), Geraerts & Joosse (1984; basommatophorans) and Tompa (1984; stylommatophorans). Clear trends in the evolution of the pulmonate reproductive system are apparent with ellobiids having the most primitive form. Morton (1955a) considered ellobiids to be phylogenetically near the point where opisthobranchs and pulmonates separated from caenogastropods. Although the primitive ellobiid reproductive system has a number of features in common with the prosobranch system, four specialised features are also present (Morton 1955b): hermaphroditism, separation of the albumen gland from the gonoduct, the development of the bursa copulatrix with an elongated duct, and a retractile, internal penis. The basal ellobiids have an open ciliated groove on the outside of the neck through which autosperm pass from the genital opening to the penis, and in the more advanced forms the ciliated groove is elaborated into a completely enclosed vas deferens. The degree of division of the gonoduct into separate male and female components is variable, but even in the primitive forms there are mechanisms that maintain the separation of oocytes and autosperm. The mechanisms range from simply being separate ciliated tracts within a common gonoduct to completely independent ducts leading to separate male and female apertures.

Pulmonates have some of the most complex invertebrate reproductive systems, and there is considerable variation among groups. Variability also occurs within families and in some groups is an important taxonomic tool at generic and specific levels. With such variation, it is difficult to generalise, but Geraerts & Joosse (1984) described a 'typical' basommatophoran reproductive system (Fig. 14.32A). Further details are presented in Chapter 17 of this volume.

Both male and female gametes are produced in a single ovotestis closely associated with the digestive gland in the upper shell whorl; the two organs cannot be easily separated. In terrestrial slugs, where the ovotestis is somewhat separate from the digestive gland, the excised gonad has been utilised in several studies. A single hermaphroditic gonoduct leads forward from

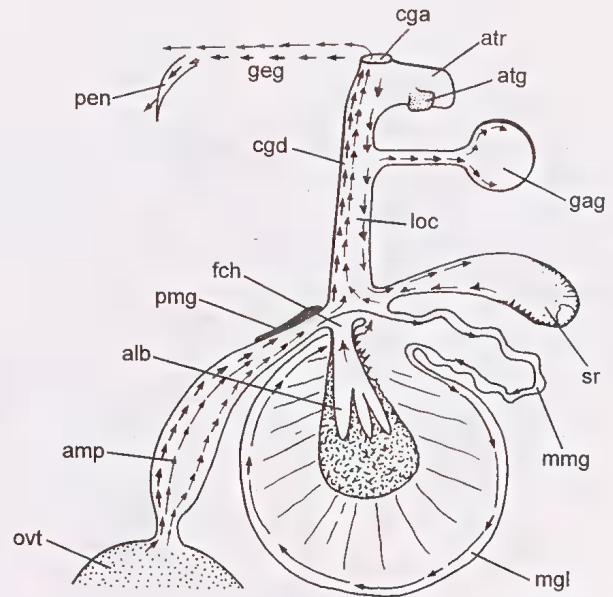


Figure 14.30 A representative opisthobranch reproductive system, as in the anaspidean *Phyllaplysia taylori* (Aplysiidae). alb, albumen gland; amp, ampulla; atg, atrial gland; atr, atrium; cga, common genital aperture; cgd, common genital duct; fch, fertilisation chamber; gag, gametolytic gland or copulatory bursa; geg, genital groove; loc, location of penis tip in copulation; mgl, mucous gland; mmg, membrane gland; ovt, ovotestis; pen, penis; pmg, postampullar gland; sr, seminal receptacle. (After Beeman 1970) [M. Thompson]

the ovotestis to the area where the hermaphroditic gonoduct separates into individual male and female ducts, a structure known as the carrefour (Fig. 14.32C). The albumen gland enters the carrefour as do one or more fertilisation pouches. As in opisthobranchs, the female portion of the reproductive system is large and glandular. It secretes nutritive and protective material associated with the fertilised ova and has specialised areas in which allosperm are received and stored. The bursa copulatrix and albumen gland are present in all basommatophorans and there may be one, or even two, mucous glands. In terrestrial forms, more complex capsules have developed that withstand the more rigorous environment, and the female portion of the reproductive system is more complex.

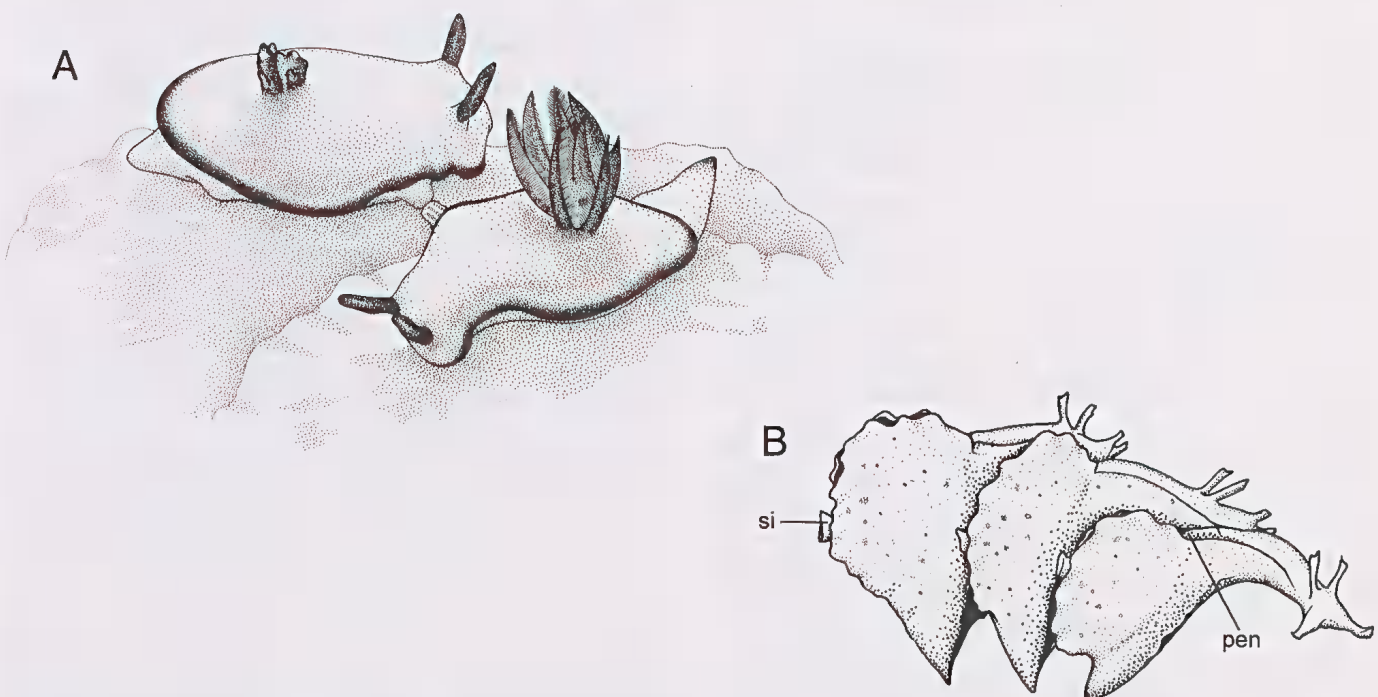


Figure 14.31 Copulation in opisthobranchs. A, *Chromodoris* sp. (Chromodorididae). B, a copulatory chain of *Aplysia* sp. (Aplysiidae). pen, penis; si, siphon. (A, after photograph by C. Bryce; B, as modified by Beeman 1970, after Eales 1921) [A, C. Eadie; B, M. Thompson]

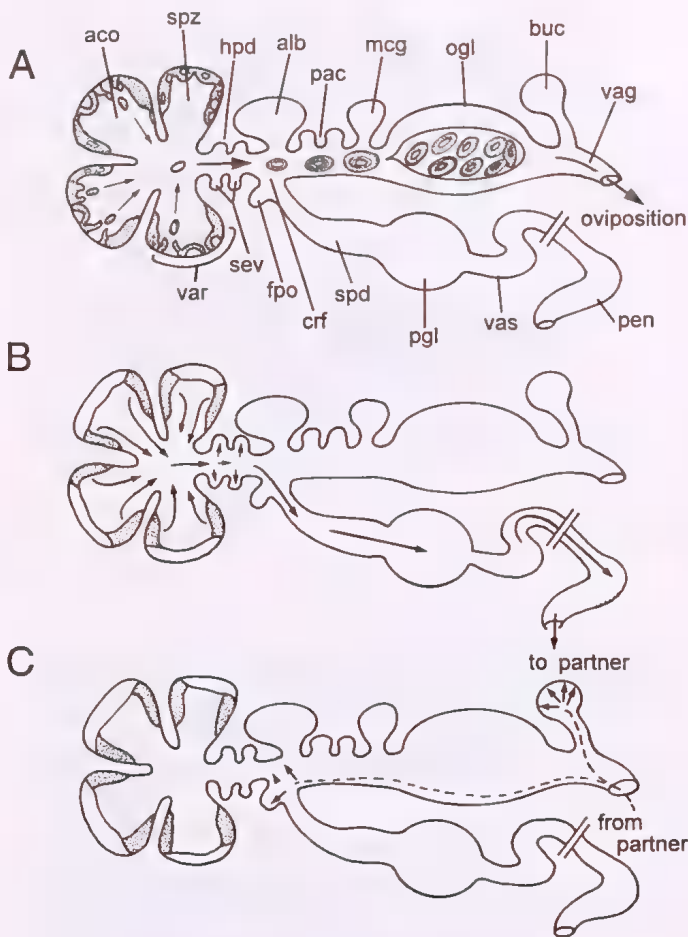


Figure 14.32 The basommatophoran reproductive system, diagrammatic representation, based on *Lymnaea stagnalis* (Lymnaeidae). A, ovulation, egg and egg mass formation. B, endogenous sperm pass from storage in the seminal vesicle to the functionally female copulation partner. C, most of the exogenous sperm is hydrolysed in the bursa copulatrix, some is transported to the fertilisation pocket where it remains until oocytes are shed ready for fertilisation. aco, acinus of the ovotestis; alb, albumen gland; buc, bursa copulatrix; crf, carrefour; fpo, fertilisation pocket; hpd, hermaphroditic duct; mcg, muciparous gland; ogf, oothecal gland; pac, pars contorta; pen, penis; pgl, prostate glands; sev, seminal vesicle; spd, sperm duct; spz, spermatozoa; vag, vagina; var, vitellogenic area; vas, vas deferens. (After Geraerts & Joosse 1984) [M. Thompson]

The male pulmonate reproductive structures are relatively simple, compared to the female portion of the reproductive system (Fig. 14.32B). Autosperm are stored in the hermaphrodite duct, which can become quite swollen by the stored sperm. Sperm are moved through the sperm duct to the base of the penis. The penis is everted during copulation and sperm move through the vas deferens to the partner. In some genera the penis is armed with darts that are thought to provide sensory stimulus prior to copulation (Goddard 1962), although their function has not been clearly demonstrated. Some species lack a penis, and sperm transfer may be accomplished by enclosing sperm in a jelly mass or a fully developed spermatophore.

Courtship behaviour is elaborate in the Stylommatophora, and often occurs nocturnally. In the introduced European slug *Limax maximus*, for example, the two individuals copulate on a vertical surface with their bodies intertwined (Duncan 1975). The animals can fall off the surface but are held by a slimy thread for the duration of copulation. The penes intertwine and fertilisation is reciprocal. In pulmonates copulation is typically reciprocal but may be either sequential or simultaneous. Copulatory times usually range from 30–80 min, but vary from a few minutes to as long as 12 hours (Duncan 1975). Although courtship and copulation may require considerable periods of time, the actual time required for sperm transfer is only a fraction of the total.

Deposition of Eggs

With the variety of reproductive morphologies found among gastropods, it is not unexpected that the form in which eggs leave the female is similarly varied, and that there should be a variety of different kinds of egg masses. As mentioned previously, the simplest form of gamete release occurs in patellogastropods and vetigastropods where many species spawn into the water column and fertilisation is external. External fertilisation is uncertain and the developing veligers are planktonic, but dependent on yolk reserves for their nutrition. Only a minute proportion of the eggs produced are actually fertilised and survive the planktonic stage to metamorphose into benthic juveniles. To offset this, tremendous numbers of eggs are produced; for example, millions of eggs can be produced by a single female abalone during the reproductive season.

In more advanced gastropods there is a trend towards production of fewer eggs and the development of mechanisms that ensure a high proportion of survivors. Fertilisation is internal in the Neritoidea, and in all caenogastropods, a process which obviates the losses inherent in planktonic fertilisation. Two additional mechanisms reduce larval losses in higher gastropods: provision by the female of a nutritive source for the developing embryo, and development of egg capsules from which the young emerge at a late stage of development. These mechanisms increase survivorship of the young and thus allow females to produce fewer eggs.

Nutrients to be utilised by the developing embryo are provided in the form of albumen which surrounds the fertilised egg before it is encased by a membrane. Young can still be released from the capsule at the veliger stage. Two types of veliger are produced. Planktotrophic veligers utilise nutrient resources in the albumen/yolk initially and then feed in the plankton, whereas lecithotrophic veligers have sufficient resources provided by the female to complete their planktonic development without external food supplies. In many caenogastropods the planktonic stage is completely suppressed and the young emerge as crawling juveniles. Some caenogastropods deposit eggs in the egg case which do not develop, termed nurse eggs, as a source of nutrition for the developing young (see Fig. 1.20C, D). As the viable embryos develop, they feed on the nurse eggs. The number of nurse eggs in a capsule is variable but as many as several hundred for each developing egg have been recorded.

Capsules are produced by the capsule gland in the oviduct after the egg membranes have been added and as the fertilised eggs leave the female. Capsules are still soft when they emerge and are pliable enough to be moulded by the foot. A pedal gland on the foot of neogastropods moulds the capsule to the proper shape.

A number of caenogastropods, for example, some species of *Littorina*, expel pelagic capsules into the surrounding water but most capsules are attached to the substratum. Capsules vary in shape and size (Fig. 1.20), and are often easily recognisable, sometimes even to species. The number of eggs per capsule and number of capsules deposited by a female vary among groups. Even within a species substantial variation can occur, associated with the size of the female and environmental conditions. Development time of embryos within the capsule ranges from a few days to several months. Species in which the young develop through the larval stages and emerge as crawling juveniles tend to remain longer in the capsule than those released at earlier stages.

Most opisthobranchs deposit egg masses in strings, bound together by mucus, and attached to the substratum. The shape of the egg mass is characteristic in a number of groups. In most taxa the young emerge as veligers, although direct development is known for some species. Rose (1985) surveyed the spawn masses and developmental stage at release of 29 opisthobranch species in New South Wales: 21 had planktotrophic veligers, two developed lecithotrophically, and six were direct developers. Eggs are also deposited in gelatinous masses in marine pulmonates and emerge as veligers. In more advanced pulmonates in freshwater and on land, the veliger stage is suppressed and the young emerge as juveniles.

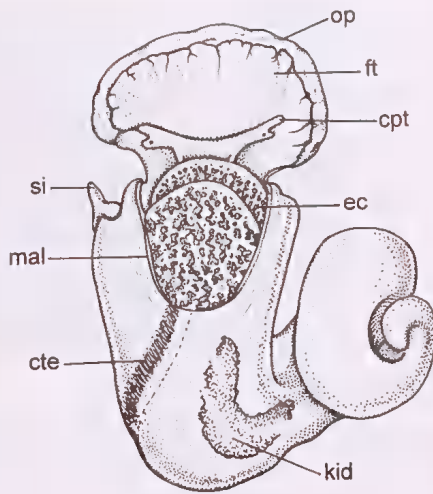


Figure 14.33 A female *Coralliophila* sp. (Muricidae), the mantle lining removed to show the location of the egg capsules. cpt, cephalic tentacle; cte, ctenidia; ec, egg capsules; ft, foot; kid, kidney; mal, cut edge of mantle lining; op, operculum; si, siphon. (After Wells & Lalli 1977) [M. Thompson]

Most gastropods are oviparous, depositing egg masses from which the young emerge on their own at different developmental stages depending on the species or group. In most taxa, the eggs are abandoned by the female after they are deposited but in some taxa, for example, some cowries, they are tended by the female. A few gastropods have more specialised systems of dealing with the eggs. For example, in the architectonicid genus, *Philippia*, eggs develop in the umbilicus of the female shell (Robertson 1970). Embryo retention occurs in various forms in all major gastropod groups. Embryos of hipponicids, calyptraeids and coralliophilines are deposited in capsules that are retained in the mantle cavity of the female (Fig. 14.33); cephalic brood pouches are used in planaxids (Houbrick 1987). In the thecosome *Limacina inflata*, the young are also retained in the mantle cavity but are attached to the mantle itself and remain there until released as veligers. In the related *L. helicoides*, embryos are retained in capsules in the oviduct and emerge as juveniles (Lalli & Wells 1978). Similar retention of embryos in the oviduct of females is known in some caenogastropods, such as the freshwater Viviparidae and some pulmonates.

Reproductive Periodicity

In general, tropical marine mollusc species are thought to spawn for extended periods of the year, whereas the reproductive season of species in temperate waters is shorter. There is little information on reproductive seasonality of tropical species in Australia, but several studies on temperate forms show that even in one area, there are considerable differences in the spawning seasons of various species. Variability in the spawning cycles of ten vetigastropod and patellogastropod species at a single locality in Sydney has been demonstrated (Underwood 1974). Differences also occur between congeners. In South Australia, the abalone, *Haliotis cyclobates*, spawns from October to January, *H. laevigata* from October to June, and *H. roei* is active throughout the year (Shepherd & Laws 1974). The reproductive periodicity of one species may also vary from one locality to another.

EMBRYOLOGY

Early Development

Sexes are separate in most gastropods, but a few species are known to be parthenogenetic, with no males in the population (Stoddart 1985). Egg size varies considerably, depending on the amount of nutritive material associated with the developing embryo.

Gastropods, and indeed all molluscs, are characterised by a spiral cleavage (see Fig. 1.18). The formation of polar lobes is a noticeable feature of early development in many caenogastropods. In the first division a lobe forms on one of the two blastomeres at the vegetal pole. The connection between lobe and blastomere initially becomes constricted but the lobe later fuses with the blastomere. On subsequent divisions the polar lobe reforms from one of the cells divided from the cell in which the lobe last occurred. Polar lobe formation can continue as late as the fifth division. Its occurrence appears to be critical to the proper development of the embryo but the mechanism by which the polar lobe affects development is not known. Polar lobe formation does not occur in patellogastropods, vetigastropods, opisthobranchs or pulmonates, but is especially well developed in neogastropods (Verdonk & Biggelaar 1983).

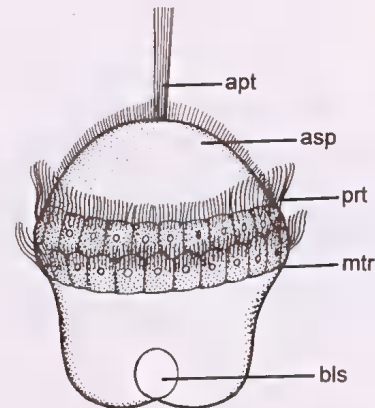


Figure 14.34 Trochophore larva of a species of *Patella* (Patellidae). apt, apical tuft; asp, apical sensory plate; bls, blastopore; mtr, metatroch; prt, prototroch. (After Patten 1886, in Hyman 1967) [M. Thompson]

Larval Stages

The trochophore, found in most other classes, is the first of two larval stages (Fig. 14.34); the second is the veliger. The trochophore lacks a shell and is characterised by its biconical shape. A complete U-shaped gut is present, with the mouth at the upper centre of the body and the anus near the bottom. A row of locomotory cilia, the prototroch, encircles the body just below the level of the mouth. A second row of cilia, the paratroch may occur ventrally, encircling the anus, and an apical tuft of cilia is present on the dorsal end. The trochophore is not restricted to molluscs, but is also a characteristic stage in the development of annelids and some other groups.

A free swimming trochophore stage occurs only in patellogastropods and vetigastropods which shed their gametes into the sea. When early development takes place in the capsule, the trochophore stage occurs in the capsule (Hyman 1967).

The great majority of gastropod species – most caenogastropods and opisthobranchs and nearly all pulmonates – begin a benthic existence at metamorphosis initiated in the capsule before hatching. In *Littorina scabra* and *Planaxis* in Australia, the embryos develop in the female mantle cavity and are released either as juveniles or short-lived planktonic veligers. In gastropods with a shell, there is often a distinct transition between the larval shell and the juvenile shell of the adult (Fig. 14.36A, B). In opisthobranchs which lack shells as adults, the larval shell is simply lost at metamorphosis.

The veliger is the typical gastropod larval stage, and is found only in molluscs (Fig. 14.35). It is characterised by a flattened velum consisting of two ciliate paddles at the anterior of the body with a pair of eyes and tentacles. Most gastropods have a simple velum, but in some species each paddle is subdivided into two four, six or

more lobes. There are two main rows of cilia near the margin of the velum separated by a food groove and additional secondary rows may also be present. The foot begins to develop while the velum is still present. In the late veliger stage the animal is often able to crawl on the bottom using the foot, or swim with the velum. As the foot develops, the velum is eventually lost, usually through resorption. A shell is present in the veliger stage into which the entire animal can withdraw, and an operculum is always present. Most of the larval organs continue to grow and are functional in the adult. A notable exception, however, is the larval heart which provides circulation to the velum. This heart co-occurs in the veliger stage with the incipient adult heart, but along with the velum is lost at metamorphosis.

Development Times

The length of larval life is variable. In species with a brief planktonic larval life, the veliger stage may be reached within a day or two after the egg hatches and the entire planktonic stage may last only a week. Other gastropods remain in the plankton as veligers for periods as long as a year or more.

Veliger larvae are of two types: planktotrophic, which do feed whilst in the plankton; and lecithotrophic, which do not feed, although they are present in the plankton (Bouchet 1989). The Australian malacologist Charles Hedley (1899) drew attention to the consequences of developmental type in molluscs. The critical observation was the 'absence of certain forms [*Melo*, *Voluta* and *Nautilus*] which were abundant on the continental islands nearest Funafuti, [rather] than the presence of others'. Hedley surmised that distance is 'an insuperable barrier' to these which lack a veliger larval stage and which have bulky eggs, but that distance does not limit *Mitra*, *Conus* or *Cypraea*, with their larval swimming stages. He supposed 'that the bulk of the molluscan fauna reached Funafuti in the larval swimming stage'.

In an elegant discussion of life history and biogeographic patterns in *Conus*, Kohn & Perron (1994) found that species with two-dimensional ranges in oceanic islands have small eggs and hence longer precompetent planktonic durations than those with more linear ranges along continental shorelines, and non-planktonic development is more characteristic of species in the former environment.

LARVAL LIFE

Veliger

Many marine gastropods have a planktonic veliger larval stage and benthic juvenile and adult stages. Veligers are subject to heavy predation, transport away from suitable habitat by ocean currents, and lack of suitable substratum on which settlement can occur. One way of compensating for this loss is by the production of large numbers of larvae. Gastropods with direct-developing larvae produce few eggs, perhaps 10 to 500, whereas some of those with planktonic larvae can produce thousands of eggs.

A planktonic veliger larval stage offers two benefits, one associated with food resources, the other with distribution. Planktotrophic veligers are filter feeders on phytoplankton and small particles floating in the water, whereas the benthic adults may be grazers or carnivores. These veligers thus typically utilise a food resource quite different from that of the adult. The veliger stage is also readily distributed. Even though the veligers are able to swim they cannot do so against a sustained current and are carried by water movements into areas which may be far removed from those in which the parents are located. Dispersal results in genetic interchange between distant populations. In the Indo-West Pacific, for example, some gastropods distributed along the coastline of tropical Australia also occur throughout the Indo-West Pacific between the east coast of southern Africa and the Hawaiian Islands.

Little is known about the distances that individuals of different species can be transported as veligers, but clearly species which live longer in the plankton will move further than short-lived species. Recent evidence indicates that abalone, which typically have a planktonic life span of only about a week, may move only a few tens of metres from where the adults spawned (Prince, Sellers, Ford & Talbot 1987). Whether other short-term veligers move for such short distances is not yet known. However, long-lived veligers, which may remain in the plankton for a year or more, do move considerable distances, and even cross oceans (Thorson 1961; Scheltema 1971, 1978; Scheltema & Williams 1983).

Marine Species Without Veligers

A substantial number of marine gastropods do not have a planktonic veliger stage in their development. Gene flow between populations is not readily maintained under such circumstances, and there is an increased tendency for the formation of distinct genetic forms in different areas. This is particularly obvious in the volutes, a diverse group in Australia (see for example Wilson & Gillett 1971). Distribution mechanisms in species without a planktonic stage are not well understood, but there is evidence that rafting occurs, either of adults or of egg masses attached to floating objects.

Non-marine Species

With the exception of insular Neritidae, the veliger stage is suppressed in freshwater and terrestrial gastropods. In freshwater species, a planktonic veliger would be washed downstream in flowing water and in terrestrial forms there is simply no opportunity for a veliger to occur. The lack of a dispersive stage means that non-marine gastropods are more limited in distribution than marine species. Many hydrobiids are restricted to very small areas, for example, a single stream. Ponder *et al.* (1993) demonstrated the considerable genetic differentiation between habitats, even within species (Ponder *et al.* 1994). Solem (1988) showed a classic pattern of restricted ranges of camaenid land snails in the Ningbing Ranges and Jeremiah Hills of the Kimberley area of Western Australia. The area, about 52 km in length, consists of a series of small limestone hills, most less than 500 m wide and less than 80 m high, and isolated from each other by open sandy areas. Twenty-eight camaenid species, primarily in three genera, occur in the hills. Most of the species are allopatric. The average range of these snails is only 1.8 km with a total area of only 0.8 km². Eight species have a total range of less than 1.0 km, and one species has a range of 0.1 km.

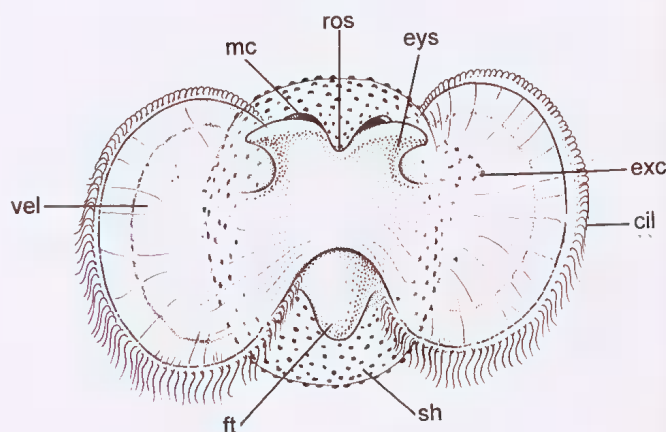


Figure 14.35 Veliger larva of *Coralliophila* species (Muricidae). cil, cilia on velum; exc, extension of columella; eys, eye spot; ft, foot; mc, mantle cavity; ros, rostrum; sh, shell; vel, velum. (After Wells & Lalli 1977)

[M. Thompson]

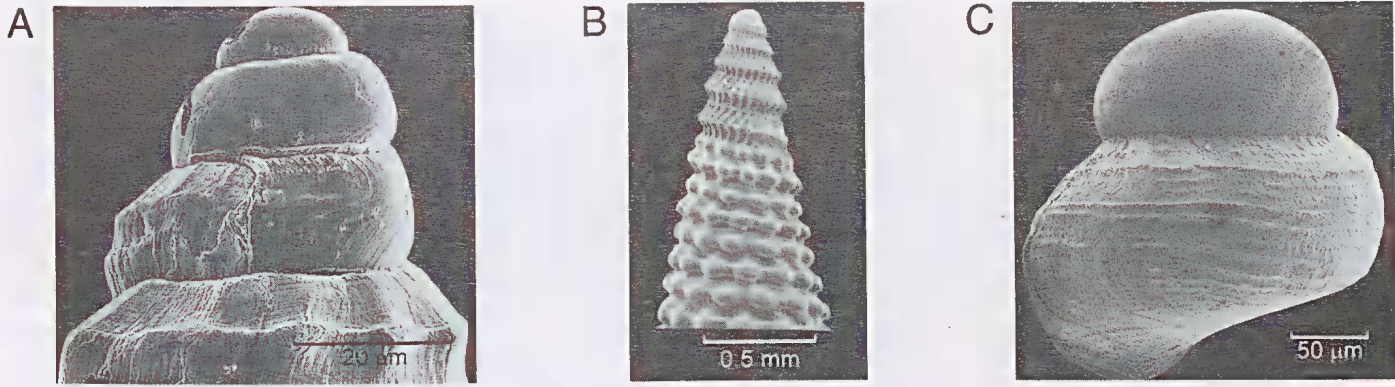


Figure 14.36 A, B, protoconchs showing whorls; note the sharp transition between the embryonic and the juvenile sculpture: A, *Cacozeliana granaria* (Cerithiidae); B, *Mastoniaeforis* cf. *chaperi* (Triphoridae). C, late embryonic shell of *Fissilabia decollata* (Planaxidae) removed from the brood pouch before hatching. (A, from Houbrick 1993; B, from Marshall 1983; C, from Houbrick 1987)

DISTRIBUTION

Marine Distribution

Three zoogeographic elements can be recognised in the marine gastropod fauna of Australia: tropical, warm temperate species and east or west coast endemics. In general, the shallow-water benthic marine gastropod species of Australia have ranges which extend over hundreds of kilometres. Only a small fraction of the species have restricted ranges. Some of these have been described only recently and their known ranges will undoubtedly be increased as new information is gathered.

The tropical fauna is distributed across the north coast of the continent, from North West Cape in Western Australia to about 26°S latitude on the Queensland coast and the southern tip of the Great Barrier Reef. The gastropods of this area are part of the vast Indo-West Pacific faunal region which extends over large areas of the tropical Indian and Pacific Oceans from the east coast of Africa eastwards to the Hawaiian Islands. Species occurring along the north coast of Australia often also occur in many other areas of the Indo-West Pacific. The money cowrie, *Cypraea moneta*, for example, is widespread in northern Australia, from Rottnest Island, off Perth, Western Australia, to New South Wales. It is also found through the Indo-West Pacific from the Natal coast of South Africa to the Red Sea, southern Japan, Polynesia, Hawaii, and even across the east Pacific barrier, to Cocos Island and the Galapagos Islands.

The warm temperate fauna of the south coast of Australia is largely unique to Australia. Species in this fauna tend to be widespread from New South Wales to southern Western Australia, though a number have restricted ranges. A few species, particularly among the opisthobranchs, occur throughout the Southern Hemisphere in temperate areas. The warm temperate marine gastropods of southern Australia are largely distinct from those of New Zealand though some species are found in both areas. Notable among these are the common rocky shore gastropods *Nerita atramentosa* and *Nodilittorina unifasciata*, though the latter species is considered to be represented by separate subspecies in Australia and New Zealand (Rosewater 1970).

Although the gastropods of southern Australia are mostly distinct from those of southern Africa and New Zealand, there are some interesting overlaps. Five temperate South African species have been recorded in the south-western corner of Western Australia. These appear to have been natural introductions, although only one is known to have established viable populations in Australia (Wells & Kilburn 1986; Willan 1987). The New Zealand potamidid *Zeacumantus subcarinatus* is common on rocky shores in Sydney Harbour, apparently the result of human introduction through shipping (Powell 1979).

The east and west coasts of Australia are faunal overlap zones where northern tropical species mix in varying proportions with the southern warm temperate species. A few gastropod species are endemic to either the east or west coast overlap zones. For example, on the west coast, the cowrie *Cypraea rosselli* is endemic to the area between Geographe Bay and Shark Bay, and the potamidid *Pyrasmus ebeninus* is an east coast endemic which is common on the muddy bottoms of mangrove forests. Species endemic to the east and west coasts of the continent are few in number, many are abundant and important ecologically.

There are two contrasting views on how the shallow-water benthic marine fauna of Australia should be divided regionally. Ekman (1953), Wilson & Gillett (1971) and Wilson & Allen (1987) followed the division outlined above, that is, the fauna is basically a section of the tropical Indo-West Pacific on the north coasts and a warm temperate fauna unique to Australia on the south coast. The east and west coasts of the continent are overlap zones with a small proportion of endemic species on each coast. Wilson & Gillett (1971) suggested that further faunistic subdivision would emphasise differences between regions and obscure the broad faunal overlaps.

An alternative view is to subdivide the coastline into distinctive regions. Hedley (1904, 1926) divided the Australian marine fauna into two tropical and two temperate provinces. The coastline between Geraldton and Cape York was named the Dampierian Province and from Cape York southwards the Solanderian Province. The warm temperate fauna on the south coast was divided into an Adelaidean region in the west and a Peronian province in the east. The general boundaries and overlap areas have been disputed, as discussed by Ponder & Wells (see Chapter 1).

The differences of opinion as to the most appropriate division of the Australian coastline into biogeographical regions arise for two reasons. Firstly, different groups of organisms show different patterns, and secondly, taxonomic judgments become important in delineating biogeographic patterns because the determination of provinces is based on the relative number of forms unique to an area. Marsh (1976) favoured retention of distinct Banksian and Dampierian regions because 20% of the shallow-water asteroids of northern Western Australia are endemic to the waters west of Torres Strait. Wells (1980) found that 88% of the 'prosobranch' gastropods investigated in northern Western Australia also occur in either Queensland or in adjacent parts of the Indo-West Pacific. Many gastropods, even such well known species as *Thais orbita* and *Turbo torquatus*, were originally distinguished as separate species in eastern and western Australia but are now considered representative of single widespread species.

The discussion above concerns the benthic marine molluscs of shallow waters, the areas that are best known, and that can be reached via the intertidal zone, snorkelling or scuba diving in

14. CLASS GASTROPODA

waters up to 50 m deep. The bottom can be sampled at greater depths using trawls or dredges operated from small boats. The exact depth limit of shallow-water gastropods is poorly defined.

Little is known of the molluscs living at greater depths off the Australian coasts. For example, an extensive trawl program on the North West Shelf, off the north coast of Western Australia, in the early 1980s revealed a previously unknown fauna on the continental slope at depths of 350 to 500 m. Among the variety of animals collected were many gastropods, of which several were new records for Australia. The overall fauna has not been examined in detail, but it is clear that it has close affinities with the fauna in the region from Japan to the Philippines (Kosuge 1985). The geographic range of the deep water fauna is not known. Preliminary trials made off Perth have uncovered some of the same species, suggesting that the fauna extends well down the west coast of Western Australia.

Over 98% of the marine mollusc species of the world have benthic juvenile and adult stages. Fewer than 150 gastropod species (Heteropoda, Thecosomata, Gymnosomata and a few nudibranchs) are holoplanktonic, completing their entire life cycle in the plankton.

Three biogeographically separate groups of planktonic organisms can be recognised: tropical, temperate and polar. Within these broad zones, defined largely by temperature, species are widespread and often occur worldwide in areas with the appropriate temperatures. Some of the colder water species are thought to be bipolar, occurring in the northern and southern temperate or polar areas but not in the intervening tropics, but Gilmer & Lalli (1990) have shown that at least in the genus *Clione* there are separate species in the Northern and Southern Hemispheres. The holoplanktonic molluscs recorded from the waters around Australia are almost all tropical species, including those found off the southern coast of the continent. Further south, temperate species occur, two of which, *Limacina retroversa* and *L. helicina*, are recorded from Tasmania and Victoria (Wells 1989).

A very few molluscs are neustonic, actually living on the surface of the sea. They include species of *Janthina* and the small nudibranch family Glaucidae. Both groups occur in tropical and warm-temperate seas, although, like the planktonic molluscs, they have been found along the south coast of Australia.

Non-marine Gastropod Distribution

In contrast to marine gastropods, non-marine species appear to be much less diverse and have relatively restricted ranges. Most of the families that occur in Australia also occur on other continents, but there is a substantial degree of endemism at the generic and species level.

Our lack of knowledge of Australian non-marine molluscs is amply illustrated by the monographic works on camaenid land snails of the Kimberley region of Western Australia by Solem (1979, 1981a, 1981b, 1984, 1985, 1988). Solem monographed 139 species in 29 genera, of which 89 species and 12 genera were previously undescribed, and suggested (1985) that only half of the living species have now been described. Similar proportions of un-named taxa have been estimated for two other diverse families, the terrestrial Charopidae (128 named species-group taxa) and the freshwater Hydrobiidae (117 named species-group taxa) (see Conservation in Chapter 1; Ponder 1994; Stanisic 1994). In all, some 990 non-marine gastropod taxa are recorded for Australia (see Table 1.7, based on Smith 1992 and subsequent papers).

Most of the work published to date on the zoogeography of Australian non-marine molluscs has referred separately either to freshwater or to terrestrial forms, but has not considered the two groups together. Iredale & Whitley (1938) first divided the continent into a variety of freshwater regions based on molluscs and fish. Later modifications were made by Iredale (1943), Whitley (1947) and McMichael & Hiscock (1958). Tate (1887)

was the first to attempt to outline zoogeographical regions for the Australian terrestrial fauna. Subsequently rearrangements were made by Hedley (1894a), Iredale (1937a, 1937b) and McMichael & Iredale (1959). The two sets of zoogeographic regions used entirely distinct series of names for the different regions, despite the fact that Iredale & Whitley (1938) and McMichael & Iredale (1959) recognised that the patterns for freshwater distribution are in general agreement with those of terrestrial snails. Smith & Kershaw (1979) outlined the six faunal regions for non-marine molluscs that are adopted in this volume (see Biogeography in Chapter 1).

FOSSIL HISTORY

The major groups of gastropods are not equally represented in the fossil record. Vetigastropoda and Caenogastropoda, with their heavy shells, are the most diverse groups in fossil assemblages, but species with small shells are not well recorded. Because of their reduced shells, shelled opisthobranchs are generally scarce in the fossil record, although some are common as fossils. Few fossil marine pulmonates are known; pulmonates inhabit high tidal areas or rocky shores, and are rarely fossilised. The land snail fauna in Australia is diverse, but few fossil species have been recorded, because of the lack of suitable deposits.

The first Australian fossil gastropod, *Umbilia eximia* (Cypraeidae), was described by G. Sowerby in de Strzlecki's (1845) report. Together Cotton (1964) and Darragh (1970) presented a complete list of other mollusc taxa described from the Australian Tertiary – 24 scaphopods, 16 cephalopods, 76 chitons, 420 bivalves and 1035 gastropods.

Study of Tertiary gastropods was intense from 1870 to 1899 when over half (807) the presently known taxa were described, largely the result of the work of R. Tate who alone described more than 400 species and subspecies. A relatively quiescent period followed until the 1940s when a second, smaller increase in new descriptions occurred as the result of the work of A.W.B. Powell and N.H. Ludbrook. Relatively few new taxa have been published since 1950, and much of the published work has dealt with faunas and revisions of groups rather than descriptions of new taxa. Darragh's (1988) treatment of the family Volutidae is an important example of a recent revision of fossil species.

Our present understanding of Australian fossil Gastropoda is patchy, and much of the published work refers to only a few areas. Before 1950 work was concentrated largely on the south-eastern corner of the continent, where Victorian localities such as Muddy Creek received most attention; consequently the fauna of this area is relatively well known. Singleton, in 1941 and 1945, provided important summaries of the knowledge of Australian geology and fossils at that time.

More recently work on fossil molluscs extended westward. The Roe Plains which extend across the South Australian Bight were recorded as fossiliferous by Tate (1894). However systematic collections were made only some 60 years later by Ludbrook. She worked extensively on Roe Plains fossil molluscs over the next quarter of a century and published a series of important papers. The work reached its climax with the publication (Ludbrook 1978) of a monograph on the Roe Plains molluscs. Subsequently, a semipopular book (Ludbrook 1984) on the Quaternary molluscs of South Australia was published. The importance of Ludbrook's work was recognised by the publication of a memorial volume in her honour (Lindsay 1985). Aside from the Roe Plains, little is known of the fossil gastropods of Western Australia, although Kendrick (1960, 1977a, 1977b) and Darragh & Kendrick (1980) have published several recent reports.

Our knowledge of the distribution of gastropod species through time is also patchy. The Palaeozoic fauna is the least well understood; few species of gastropods have been described. Preliminary work was done near the turn of the 20th Century but little was published subsequently until a series of papers in the 1970s by Tassell (1976, 1977, 1978) on the early Devonian

Gastropods from three sites in Victoria. The genera are loosely defined and their placements are tentative. Information on Tertiary molluscs is relatively good. Darragh (1970) listed over 1000 species and subspecies.

Gastropods of the more recent sediments of the Quaternary are the best known. Species from these relatively recent geological times have a considerable overlap with extant species. Of the 259 species and subspecies of the Roe Plains molluscs, which Ludbrook (1978) considered to be early Pleistocene, 65% to 70% are extant.

The gastropods and other molluscs of Quaternary sediments have been used to examine changes in shallow-water marine environments. Ludbrook (1978), for example, suggested that the Roe Plains were once submerged, with the Hampton Range to the north being the shoreline. From the composition of the fossil fauna, she suggested that the Roe Plains were a shallow, sandy

embayment with some intertidal mudflats. The presence of a few tropical and subtropical species in the Roe Calcarene, species which have present day distributions farther north, suggests that warmer sea surface temperatures prevailed when the shells were deposited.

Hodgkin & Kendrick (1984) studied the fossil shells and present distributions of molluscs, primarily species of the bivalve genus *Katelysia*, in estuaries in the south-western corner of Western Australia and showed that the fauna of estuaries on the lower coast earlier than 4500 years ago was similar to that found in a number of present day estuaries on the south coast. About 4500 years ago a sudden change occurred in the fauna of the lower west coast estuaries, when many of the euryhaline marine species living in the estuaries became extinct on the west coast. Subsequently, the molluscan fauna of these estuaries has been dominated by small, euryhaline gastropods and bivalves.

LITERATURE CITED

- Allan, J. (1950). *Australian Shells: with related animals living in the sea, in freshwater and on the land*. Georgian House : Melbourne xix 470 pp.
- Allan, J. (1956). *Cowry Shells of World Seas*. Georgian House : Melbourne x 170 pp.
- Andrews, E.B. (1988). Excretory systems of molluscs. Pp. 381–448 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca*. Vol. 11. *Form and Function*. Academic Press : New York
- Angas, G.F. (1867a). A list of species of marine mollusca found in Port Jackson harbour, New South Wales and adjacent coasts, with notes on their habits, etc. Part 1. *Proceedings of the Zoological Society of London* 1867: 185–233
- Angas, G.F. (1867b). A list of species of marine mollusca found in Port Jackson harbour, New South Wales and adjacent coasts, with notes on their habits, etc. Part 2. *Proceedings of the Zoological Society of London* 1867: 912–935
- Angas, G.F. (1871). A list of additional species of marine mollusca to be included in the fauna of Port Jackson and the adjacent coasts of New South Wales. *Proceedings of the Zoological Society of London* 1871: 87–101
- Angas, G.F. (1877). A further list of additional species of marine mollusca to be included in the fauna of Port Jackson and the adjacent coasts of New South Wales. *Proceedings of the Zoological Society of London* 1877: 178–194
- Audesirk, G.J. (1978). Central neuronal control of cilia in *Tritonia diamedea*. *Nature* 272: 541–543
- Audesirk, T. & Audesirk, G. (1985). Behavior of gastropod mollusks. Pp. 1–94 in Willows, A.O.D. (ed.) *The Mollusca*. Vol. 8. *Neurobiology and Behavior*. Part 1. Academic Press : New York
- Batten, R.L., Rollins, H.B. & Gould, S.J. (1967). Comments on the 'adaptive significance of gastropod torsion'. *Evolution* 21: 405–406
- Beeman, R.D. (1970). An autoradiographic study of sperm exchange and storage in a sea hare, *Phyllaplysia taylori*, a hermaphroditic gastropod (Opisthobranchia: Anaspidea). *Journal of Experimental Zoology* 175: 125–132
- Beeman, R.D. (1977). Gastropoda: Opisthobranchia. Pp. 115–179 in Giese, A.C. & Pearse, J.S. (eds) *Reproduction of Marine Invertebrates. Mollusca: Gastropods and Cephalopods*. Vol. 4. Academic Press : New York
- Berg, C. (1974). A comparative ethological study of strombid gastropods. *Behaviour* 51: 274–322
- Berry, A.J. (1977). Gastropoda: Pulmonata. Pp. 181–226 in Giese, A.C. & Pearse, J.S. (eds) *Reproduction of Marine Invertebrates. Mollusca: Gastropods and Cephalopods*. Vol. 4. Academic Press : New York
- Bieler, R. (1990). Haszprunar's "clado-evolutionary" classification of the Gastropoda – a critique. *Malacologia* 31: 371–380
- Bieler, R. (1992). Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics* 23: 311–338
- Bishop, M.J. (1981). The biogeography and evolution of Australian land snails. Pp. 925–954 in Keast, A. (ed.) *Ecological Biogeography of Australia. Monographiae Biologiae* 41. Junk : The Hague
- Boettger, C.R. (1954). Die Systematik der euthyneuren Schnecken. *Verhandlungen der Deutschen Zoologischen Gesellschaft in Tübingen, Supplement* 18 : 253–280
- Boss, K.V. (1971). Critical estimate of the number of Recent Mollusca. *Occasional Papers on Mollusca, Harvard University* 3: 81–135
- Boss, K.J. (1982). Mollusca. Pp. 945–1166 in Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. Vol 1. McGraw-Hill Book Co. : New York
- Bouchet, P. (1989). A review of poecilogony in gastropods. *Journal of Molluscan Studies* 55: 67–78
- Bouvier, E.L. (1887). Système nerveux, morphologie générale et classification des Gastéropodes Prosobranches. *Annales des Sciences Naturelle, Zoologie* 7: 1–510
- Burch, J.B. (1978). Outline of classification of Australian terrestrial molluscs (native and introduced). *Journal of the Malacological Society of Australia* 3: 127–156
- Cain, A.J. (1978). The deployment of operculate land snails in relation to shape and size of the shell. *Malacologia* 17: 207–221
- Carriker, M.R. (1946). Observations on the functioning of the alimentary canal of the snail *Lymnaea stagnalis appressa* Say. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 91: 88–111
- Cimino, G., De Rosa, S., De Stefano, S., Sodano, F. & Villani, G. (1983). Dorid nudibranch elaborates its own chemical defense. *Science* 219: 1237–1238
- Cook, A., Bamford, O.S., Freeman, J.D.B. & Teideman, D.J. (1969). A study of the homing habit of the limpet. *Animal Behaviour* 17: 330–339
- Cook, L. (1985). Functional aspects of trail following by the carnivorous snail *Euglandina rosea*. *Malacologia* 26: 173–181
- Cook, S.B. (1969). Experiments on homing in the limpet *Siphonaria normalis*. *Animal Behaviour* 17: 679–682
- Cotton, B.C. (1959). *South Australian Mollusca. Archaeogastropoda*. Government Printer : Adelaide 449 pp.
- Cotton, B.C. (1961). *South Australian Mollusca. Pelecypoda*. South Australian Branch British Science Guild : Adelaide 363 pp.
- Cotton, B.C. (1964). *South Australian Mollusca. Chitons*. South Australian Branch British Science Guild : Adelaide 151 pp.

14. CLASS GASTROPODA

- Cotton, B.C. & Godfrey, F.K. (1938). Part I. The Pelecypoda. Pp. 1–314 in *The Molluscs of South Australia*. Handbooks of the Flora and Fauna of South Australia. Government Printer : Adelaide
- Cotton, B.C. & Godfrey, F.K. (1939). A systematic list of the Gastropoda. The marine, freshwater and land univalve Mollusca of south and central Australia. *Malacological Society of South Australia Publication* 1: 1–44
- Cotton, B.C. & Godfrey, F.K. (1940). Part II. Scaphopoda, Cephalopoda, Aplacophora and Crepidopoda. Pp. 317–600 in *The Molluscs of South Australia*. Handbooks of the Flora and Fauna of South Australia. Government Printer : Adelaide
- Cox, J.C. (1868). *A List of Species of Marine Molluscs Found in Port Jackson Harbour and on the Adjacent Coasts*. Cox : Sydney
- Cox, L.R. (1960a). Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33: 239–261
- Cox, L.R. (1960b). General characteristics of Gastropoda. Pp. 184–1169 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part I. Mollusca*. Geological Society of America & University of Kansas Press : Boulder, Colorado & Lawrence, Kansas
- Crisp, M. (1971). Structure and abundance of receptors of the unspecialised external epithelium of *Nassarius reticulatus* (Gastropoda, Prosobranchia). *Journal of the Marine Biological Association of the United Kingdom* 61: 865–890
- Crofts, D.R. (1937). The development of *Haliotis tuberculata*, with special reference to organogenesis during torsion. *Philosophical Transactions of the Royal Society of London, Series B* 228: 219–268
- Crofts, D.R. (1955). Muscle morphogenesis in primitive gastropods and its relation to torsion. *Proceedings of the Zoological Society of London* 125: 711–750
- Currey, J.D. (1988). Shell form and strength. Pp. 183–210 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca. Vol. 11. Form and Function*. Academic Press : New York
- Currey, J.D. & Kohn, A.J. (1976). Fracture in the crossed-lamellar structure of *Conus* shells. *Journal of Materials Science* 11: 1615–1623
- Currey, J.D. & Taylor, J.D. (1974). The mechanical behaviour of some molluscan hard tissues. *Journal of Zoology, London* 173: 395–406
- Darragh, T.A. (1970). Catalogue of Australian Tertiary Mollusca (except chitons). *Memoirs of the National Museum of Victoria* 31: 125–212
- Darragh, T.A. (1988). A revision of the Tertiary Volutidae (Mollusca: Gastropoda) of south-eastern Australia. *Memoirs of the Museum of Victoria* 49: 195–307
- Darragh, T.A. & Kendrick, G.W. (1980). Eocene bivalves from the Pallinup Siltstone near Walpole, Western Australia. *Journal of the Royal Society of Western Australia* 63: 5–20
- Dudley, E.C. & Vermeij, G.E. (1989). Shell form and burrowing performance in gastropods from Pacific Panama with comments on regional differences in functional specialization. *The Veliger* 32: 284–287
- Duncan, C.J. (1975). Reproduction. Pp. 309–365 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional Anatomy and Physiology*. Academic Press : London
- Eales, N.B. (1921). *Aplysia*. *Proceedings and Transactions of the Liverpool Biological Society* 35: 183–266
- Edlinger, K. (1988). Torsion in gastropods: A phylogenetic model. Pp. 241–250 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement* 4
- Edmunds, M. (1966). Protective mechanisms in the Eolidacea (Mollusca, Nudibranchia). *Journal of the Linnean Society of London, Zoology* 46: 27–71
- Eisner, T. & Wilson, E.O. (1970). Defensive liquid discharge in Florida tree snails (*Liguus fasciatus*). *The Nautilus* 84: 14–15
- Ekman, S. (1953). *Zoogeography of the Sea*. Sidgwick & Jackson : London xiv 417 pp.
- Farmer, W.M. (1970). Swimming gastropods (Opisthobranchia and Prosobranchia). *The Veliger* 13: 73–89
- Faulkner, D.J. & Ghiselin, M.T. (1983). Chemical defense mechanisms and the evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. *Marine Ecology Progress Series* 13: 295–301
- Faulkner, D.J. & Ireland, C. (1977). The chemistry of some opisthobranch gastropods. Pp. 23–34 in Faulkner, D.J. & Fenical, W.H. (eds) *Marine Natural Products Chemistry*. Plenum Press : New York
- Fretter, V. (1939). The structure and function of the alimentary canal of some tectibranch molluscs, with a note on excretion. *Transactions of the Royal Society of Edinburgh* 59: 599–646
- Fretter, V. (1948). The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). *Journal of the Marine Biological Association of the United Kingdom* 27: 597–632
- Fretter, V. (1975). Introduction. Pp. xix–xix in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional Anatomy and Physiology*. Academic Press : New York
- Fretter, V. (1984). Prosobranchs. Pp. 1–45 in Tompa, A.S., Verdonk, N.H. & van den Biggelaar, J.A.M. (eds) *The Mollusca. Vol. 7. Reproduction*. Academic Press : New York
- Fretter, V. (1988). New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea. II. Anatomy. *Philosophical Transactions of the Royal Society of London, Series B* 318: 33–82
- Fretter, V. (1989). The anatomy of some new archaeogastropod limpets (Superfamily Peltospiracea) from hydrothermal vents. *Journal of Zoology, London* 218: 123–169
- Fretter, V. (1990). The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. *Journal of Zoology, London* 222: 529–555
- Fretter, V. & Graham, A. (1962) *British Prosobranch Molluscs. Their functional anatomy and ecology*. Ray Society : London xvi 755 pp.
- Fretter, V. & Graham, A. (1994). *British Prosobranch Molluscs. Their functional anatomy and ecology*. Ray Society : London 2nd edn xix 820 pp.
- Fretter, V., Graham, A. & McLean, J.H. (1981). The anatomy of the Galapagos rift limpet, *Neomphalus fretterae*. *Malacologia* 21: 337–361
- Gabriel, C.J. (1936). *Victorian Sea Shells: a handbook for collectors and naturalists*. *Field Naturalists' Club Victoria Handbook*. Field Naturalists' Club of Victoria : Melbourne 67 pp.
- Galbraith, R.T. (1965). Homing behavior in the limpets *Acmaea digitalis* and *Lottia gigantea*. *American Midland Naturalist* 74: 245–246
- Garstang, W. (1929). The origin and evolution of larval forms. *Reports of the British Association for the Advancement of Science* 96: 77–98
- Geraerts, W.P.M. & Joosse, J. (1984). Freshwater snails (Basommatophora). Pp. 142–207 in Tompa, A.S., Verdonk, N.H. & van den Biggelaar, J.A.M. (eds) *The Mollusca. Vol. 7. Reproduction*. Academic Press : New York
- Ghiretti, F. (1966a). Respiration. Pp. 175–208 in Wilbur, K.M. & Yonge, C.M. (eds) *Physiology of Mollusca. Vol. 2*. Academic Press : New York
- Ghiretti, F. (1966b). Molluscan hemocyanins. Pp. 233–248 in Wilbur, K.M. & Yonge, C.M. (eds) *Physiology of Mollusca. Vol. 2*. Academic Press : New York
- Ghiselin, M.T. (1966a). The adaptive significance of gastropod torsion. *Evolution* 20: 337–348
- Ghiselin, M.T. (1966b). Reproductive function and the phylogeny of opisthobranch gastropods. *Malacologia* 3: 327–378
- Gilmer, R.W. & Lalli, C.M. (1990). Bipolar variation in *Clione*, a gymnosomatous pteropod. *American Malacological Bulletin* 8: 67–75
- Goddard, C.K. (1962). Function of the penial apparatus of *Helix aspersa* Müller. *Australian Journal of Biological Science* 15: 218–232
- Golikov, A.N. & Starobogatov, Y.I. (1975). Systematics of prosobranch gastropods. *Malacologia* 15: 185–232

- Gosliner, T. (1985). Parallelism, parsimony and the testing of phylogenetic hypotheses: the case of opisthobranch gastropods. Pp. 105–107 in Vrba, E. (ed.) *Species and Speciation*. Transvaal Museum Monographs 4: Pretoria
- Gosliner, T. (1991). Morphological parallelism in opisthobranch gastropods. *Malacologia* 32: 313–327
- Gosliner, T. & Ghiselin, M. (1984). Parallel evolution in opisthobranch gastropods and its implications for phylogenetic methodology. *Systematic Zoology* 33: 255–274
- Graham, A. (1932). On the structure and function of the alimentary canal of the limpet. *Transactions of the Royal Society of Edinburgh* 57: 287–308
- Graham, A. (1948). *Form and function in the littoral gastropod*. Inaugural lecture, University of London. Birkbeck College: London 16 pp.
- Graham, A. (1949). The molluscan stomach. *Transactions of the Royal Society of Edinburgh* 61: 737–778
- Graham, A. (1985). Evolution within the Gastropoda: Prosobranchia. Pp. 151–186 in Trueman, E.R. & Clark, M.R. (eds) *The Mollusca*. Vol. 10. *Evolution*. Academic Press: New York
- Graus, R.R. (1974). Latitudinal trends in the shell characteristics of marine gastropods. *Lethaia* 7: 303–314
- Hadfield, M.G. & Switzer-Dunlap, M. (1984). Opisthobranchs. Pp. 209–350 in Tompa, A.S., Verdonk, N.H. & van den Biggelaar, J.A.M. (eds) *The Mollusca*. Vol. 7. *Reproduction*. Academic Press: New York
- Hadfield, M.G., Kay, E.A., Gillette, M.U. & Lloyd, M.C. (1972). The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology* 12: 81–98
- Hamilton, P.V. (1977). Daily movements and visual location of plant stems by *Littorina irrorata* (Mollusca: Gastropoda). *Marine Behaviour and Physiology* 4: 293–304
- Hamilton, P.V. & Ambrose, H.W. III (1975). Swimming and orientation in *Aplysia brasiliensis* (Mollusca: Gastropoda). *Marine Behaviour and Physiology* 3: 131–144
- Hamilton, P.V. & Russell, B.J. (1982). Celestial orientation by surface-swimming *Aplysia brasiliensis* Rang (Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 56: 145–152
- Haszprunar, G. (1985a). The fine morphology of the osphradial sense organs of the Mollusca. I. Gastropoda – Prosobranchia. *Philosophical Transactions of the Royal Society of London, Series B* 307: 457–496
- Haszprunar, G. (1985b). The fine morphology of the osphradial sense organs of the Mollusca. II. Allogastropoda (Architectonicidae, Pyramidellidae). *Philosophical Transactions of the Royal Society of London, Series B* 307: 457–496
- Haszprunar, G. (1985c). The Heterobranchia – a new concept of the phylogeny and evolution of the higher Gastropoda. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 23: 15–37
- Haszprunar, G. (1987). Anatomy and affinities of cocculinid limpets (Mollusca, Archaeogastropoda). *Zoologica Scripta* 16: 305–324
- Haszprunar, G. (1988a). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura (Mollusca). *Journal of Molluscan Studies* 54: 367–441
- Haszprunar, G. (1988b). A preliminary phylogenetic analysis of the streptoneurous gastropods. Pp. 7–16 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement 4*
- Haszprunar, G. (1989a). The anatomy of *Mealanodrymia aurantiaca* Hickman, a coiled archaeogastropod from the East Pacific hydrothermal vents (Mollusca, Gastropoda). *Acta Zoologica, Stockholm* 70: 175–186
- Haszprunar, G. (1989b). New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 2. Anatomy and relationships. *Contributions in Science, Los Angeles County Museum* 408: 1–17
- Haszprunar, G. (1990). Towards a phylogenetic system of Gastropoda. Part 1: Traditional methodology – a reply. *Malacologia* 32: 195–202
- Healy, J.M. (1986). Euspermatozoa and paraspermatozoa of the relict cerithiacean gastropod, *Campanile symbolicum* (Prosobranchia, Mesogastropoda). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 40: 201–218
- Healy, J.M. (1988). Sperm morphology and its systematic importance in the Gastropoda. Pp. 251–266 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement 4*
- Hedley, C. (1892). Observations on the Charopidae. Part I. *Proceedings of the Linnean Society of New South Wales* 7: 157–169
- Hedley, C. (1894a). The faunal regions of Australia. *Reports of the Australian Association for the Advancement of Science* 5: 444–446
- Hedley, C. (1894b). On some naked Australian marine Mollusca. Part I. *Proceedings of the Linnean Society of New South Wales* 9: 126–128
- Hedley, C. (1899). A zoo-geographic scheme for the Mid-Pacific. *Proceedings of the Linnean Society of New South Wales* 24: 391–417
- Hedley, C. (1904). The effect of the Bassian isthmus upon the existing marine fauna a study in ancient geography. *Proceedings of the Linnean Society of New South Wales* 28: 876–883
- Hedley, C. (1915). A preliminary index of the Mollusca of Western Australia. *Journal and Proceedings of the Royal Society of Western Australia* 1: 152–226
- Hedley, C. (1916). Studies on Australian Mollusca. Part 3. *Proceedings of the Linnean Society of New South Wales* 41: 680–719
- Hedley, C. (1918). Checklist of the New South Wales marine Mollusca. *Journal and Proceedings of the Royal Society of New South Wales Supplement* in 51: M1–M120
- Hedley, C. (1926). Zoogeography. Pp. 743–744 in Jose, A.W. & Carter, H.J. (eds) *Australian Encyclopedia Volume 2*. Angus & Robertson: Sydney 2 vols, ix 768 pp., 748 pp.
- Hewatt, W.G. (1940). Observations on the homing limpet, *Acmaea scabra* Gould. *American Midland Naturalist* 24: 205–208
- Hickman, C.S. (1980). Gastropod radulae and the assessment of form in evolutionary biology. *Paleobiology* 6: 276–294
- Hickman, C.S. (1983). Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *The Veliger* 26: 73–92
- Hickman, C.S. (1985a). Comparative morphology and ecology of free-living suspension-feeding gastropods from Hong Kong. Pp. 217–234 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and Southern China. II. Vol. 1*. Hong Kong University Press: Hong Kong
- Hickman, C.S. (1985b). Gastropod morphology and function. Pp. 138–156 in Broadhead, T.W. (ed.) *Mollusks. Notes for a Short Course. Studies in Geology 13*. University of Tennessee Department of Geological Science: Memphis
- Hickman, C.S. (1988). Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. Pp. 17–34 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement 4*
- Hickman, C.S. (1992). Reproduction and development of trochacean gastropods. *The Veliger* 35: 235–272
- Hodgkin, E.P. & Kendrick, G.W. (1984). The changing aquatic environment 7000 BP to 1983 in the estuaries of southwestern Australia. Pp. 85–95 in Hodgkin, E.P. (ed.) *Estuarine Environments of the Southern Hemisphere*. Bulletin of the Western Australian Department of Conservation and Environment No. 161
- Houbrick, J.R. & Fretter, V. (1969). Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. *Proceedings of the Malacological Society of London* 38: 415–429
- Houbrick, R.S. (1980). Observations on the anatomy and life history of *Modulus modiolus* (Prosobranchia: Modulidae). *Malacologia* 20: 117–142
- Houbrick, R.S. (1981a). Anatomy, biology and systematics of *Campanile symbolicum* with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia). *Malacologia* 21: 263–289

14. CLASS GASTROPODA

- Houbrick, R.S. (1981b). Systematic position of the genus *Glyptozaria* Iredale (Prosobranchia: Gastropoda). *Proceedings of the Biological Society of Washington* 94: 838–847
- Houbrick, R.S. (1985). Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology* 403: 1–131
- Houbrick, R.S. (1987). Anatomy, reproductive biology, and phylogeny of the Planaxidae (Cerithiacea: Prosobranchia). *Smithsonian Contributions to Zoology* 445: 1–57
- Houbrick, R.S. (1989). *Campanile* revisited: implications for cerithioidean phylogeny. *Bulletin of the American Malacological Union* 7: 1–6
- Houbrick, R.S. (1993). Phylogenetic relationships and generic review of the Bittiinae (Prosobranchia: Cerithioidea). *Malacologia* 35: 261–313
- Hughes, H.P.I. (1985). The Hong Kong Caecidae. Pp. 155–171 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and Southern China. II*. Hong Kong University Press : Hong Kong
- Hughes, R.N. & Hughes, H.P.I. (1981). Morphological and behavioral aspects of feeding in the Cassidae (Tonnacea: Mesogastropoda). *Malacologia* 20: 385–402
- Hurst, A. (1965). Studies of the structure and function of the feeding apparatus of *Philine aperta* with a comparative consideration of some other opisthobranchs. *Malacologia* 2: 281–347
- Hurst, A. (1968). The feeding mechanism and behaviour of the opisthobranch *Melibe leonina*. Pp. 151–166 in Fretter, V. (ed.) *Studies in the Physiology and Ecology of Molluscs*. Symposium of the Zoological Society of London No. 22. Academic Press : London
- Hyman, L.H. (1967). *The Invertebrates. Vol. 6. Mollusca I*. McGraw-Hill : New York vii 792 pp.
- Illert, C.R. (1981). The growth and feeding habits of a South Australian murex. *Of Sea and Shore* 12: 8–10
- Illert, C.R. (1983). The mathematics of gnomonic seashells. *Mathematical Biosciences* 63: 21–56
- Illert, C.R. (1983). Formulation and solution of the classical seashell problem. II. Tubular three-dimensional seashell surfaces. *Il Nuovo Cimento* 11D: 761–779
- Iredale, T. (1937a). A basic list of the land Mollusca of Australia. *Australian Zoologist* 8: 287–333
- Iredale, T. (1937b). A basic list of the land Mollusca of Australia. Part 2. *Australian Zoologist* 9: 1–39
- Iredale, T. (1938). A basic list of the land Mollusca of Australia. Part 3. *Australian Zoologist* 9: 83–124
- Iredale, T. (1939). Mollusca. Part 1. British Museum (Natural History), London. Great Barrier Reef Expedition, 1928–29. *Scientific Reports* 5: 209–425
- Iredale, T. (1943). A basic list of the fresh-water Mollusca of Australia. *Australian Zoologist* 10: 188–230
- Iredale, T. (1956). Charles Hedley's papers indexed. *Proceedings of the Royal Zoological Society of New South Wales* 1956–57: 118–139
- Iredale, T. & McMichael, D. (1962). A reference list of the marine Mollusca of New South Wales. *Memoirs of the Australian Museum* 11: 1–109
- Iredale, T. & Whitley, G.P. (1938). The fluvifaunulae of Australia. *South Australian Naturalist* 18: 64–68
- Jahan-Parwar, B. & Fredman, S.M. (1983). Control of extrinsic feeding muscles in *Aplysia*. *Journal of Neurophysiology* 49: 1481–1503
- Jensen, K.R. (1980). A review of sacoglossan diets, with comparative notes on radular and buccal anatomy. *Malacological Review* 13: 55–77
- Jensen, K.R. (1983). Factors affecting feeding selectivity in herbivorous Ascoglossa (Mollusca: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology* 66: 135–148
- Jensen, K.R. (1991). Foraging behaviour of two Australian species of *Elysia* (Mollusca, Opisthobranchia). Pp. 541–551 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: Marine Flora and Fauna of Albany, Western Australia, Vol. 2*. Western Australian Museum : Perth
- Jessee, W.F. (1968). Studies of homing behavior in the limpet *Acmaea scabra*. *The Veliger* 11 (Supplement): 52–55
- Jones, H.D. (1975). Locomotion. Pp. 1–32 in Fretter, V.P. & Peake, J. (eds) *Pulmonates. Vol. I. Functional Anatomy and Physiology*. Academic Press : New York
- Jones, H.D. (1983). The circulatory system of gastropods and bivalves. Pp. 189–238 in Saleuddin, A.S.M. & Wilbur, K.M. (eds) *The Mollusca. Vol. 5. Physiology. Pt 2*. Academic Press : New York
- Kabat, A.R. (1990). Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32: 155–193
- Kandel, E.R. (1979). *Behavioural Biology of Aplysia (A contribution to the comparative study of opisthobranch molluscs)*. Freeman & Co. : San Francisco xiii 463 pp.
- Kendrick, G.W. (1960). The fossil Mollusca of the Peppermint Grove Limestone, Swan River district of Western Australia. *Western Australian Naturalist* 7: 53–66
- Kendrick, G.W. (1977a). Middle Holocene marine molluscs from near Guildford, Western Australia, and evidence for climatic change. *Journal of the Royal Society of Western Australia* 59: 97–104
- Kendrick, G.W. (1977b). Fossils from the Herschell Limestone in the collection of the Western Australian Museum. *Geological Survey of Western Australia Report* 6: 87–98
- Kerkut, G. & Walker, J. (1975). Nervous system, eye, and statocyst. Pp. 165–244 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. I. Functional Anatomy and Physiology*. Academic Press : New York
- Knudsen, J. (1991). Observations on *Hipponix australis* (Lamarck, 1819) (Mollusca, Gastropoda, Prosobranchia) from the Albany area, Western Australia. Pp. 641–660 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia, Vol. 2*. Western Australian Museum : Perth
- Kohn, A.J. (1959). The ecology of *Conus* in Hawaii. *Ecological Monographs* 29: 47–90
- Kohn, A.J. (1961). Chemoreception in gastropod molluscs. *American Zoologist* 1: 291–308
- Kohn, A.J. (1970). Food habits of the gastropod *Mitra litterata* Lamarck: relation to trophic structure of the intertidal marine bench [beach] community in Hawaii. *Pacific Science* 24: 483–486
- Kohn, A.J. (1983). Feeding biology of gastropods. Pp. 1–64 in Saleuddin, A.S.M. & Wilbur, K.M. (eds) *The Mollusca. Vol. 5. Physiology. Pt 2*. Academic Press : New York
- Kohn, A.J. (1986). Slip-resistant silver-feet: shell form and mode of life in lower Pleistocene *Argyropeza* from Fiji. *Journal of Palaeontology* 60: 1066–1074
- Kohn, A.J., Myers, E.R. & Meenakshi, V.R. (1979). Interior remodelling of the shell by a gastropod mollusc. *Proceedings of the National Academy of Science* 76: 3406–3410
- Kohn, A.J. & Perron, F.E. (1994). *Life History and Biogeography: Patterns in Conus*. Oxford University Press : Oxford
- Kohn, A.J. & Riggs, A.C. (1975). Morphometry of the *Conus* shell. *Systematic Zoology* 24: 346–359
- Kornicker, L.S. (1961). Tidal responses of *Terebra salleana*. *Ecology* 42: 207
- Kosuge, S. (1985). Noteworthy Mollusca from North-western Australia. (1). Preliminary Report. *Bulletin of the Institute of Malacology, Tokyo* 2: 58–59
- Kupferman, I. & Pinsker, H.W. (1968). A behavioral modification of the feeding reflex, and central commands controlling gill and siphon movements in *Aplysia*. *Communications in Behavioral Biology* 37: 121–203
- Lalli, C.M. (1970). Structure and function of the buccal apparatus of *Clypeomorus* (Phipps) with a review of feeding in gymnosomatous pteropods. *Journal of Experimental Marine Biology and Ecology* 4: 101–118
- Lalli, C.M. & Gilmer, R.W. (1989). *Pelagic Snails. The Biology of Holoplanktonic Gastropod Mollusks*. Stanford University Press : Stanford xiv 259 pp.

- Lalli, C.M. & Wells, F.E. (1978). Reproduction in the thecosomatous pteropod genus *Limacina* (Opisthobranchia: Thecosomata). *Journal of Zoology, London* 186: 95–108
- Laseron, C.F. (1951). Revision of the New South Wales Cerithiopsidae. *Australian Zoologist* 11: 351–368
- Laseron, C.F. (1957). A new classification of the Australian Marginellidae (Mollusca) with a review of species from the Solanderian and Dampierian zoogeographical provinces. *Australian Journal of Marine and Freshwater Research* 8: 274–311
- Laseron, C.F. (1959). The family Pyramidellidae (Mollusca) from Northern Australia. *Australian Journal of Marine and Freshwater Research* 10: 177–267
- Laws, H.M. & Mincham, H. (1968). Bernard Charles Cotton (1905–1966). Obituary, bibliography and index of his scientific names. *Journal of the Malacological Society of Australia* 1(11): 10–24
- Lee, R.M., Robbins, M.R. & Palovcik, R. (1974). *Pleurobranchaea* behavior: food finding and other aspects of feeding. *Behavioral Biology* 12: 297–315
- Lever, J. (1979). On torsion in gastropods. Pp. 5–23 in van der Spoel, S., van Bruggen, A.C. & Lever, J. (eds) *Pathways in Malacology*. Junk : The Hague
- Lindberg, D. (1988). Radular evolution in the patellogastropoda. *Bulletin of the American Malacological Union* 4: 115
- Lindberg, D. & Hickman, C.S. (1986). A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). *Journal of Palaeontology* 60: 661–668
- Lindsay, J.M. (ed.) (1985). Stratigraphy, palaeontology, malacology. Papers in honour of Dr. Nell Ludbrook. *South Australian Department of Mines and Energy, Special Publication* 5: 1–387
- Linsley, R.M. (1977). Some "laws" of gastropod shell form. *Paleobiology* 3: 196–206
- Linsley, R.M. (1978a). Locomotion rates and shell form in the Gastropoda. *Malacologia* 17: 193–206
- Linsley, R.M. (1978b). Shell form and the evolution of gastropods. *American Scientist* 66: 432–441
- Linsley, R.M. & Yochelson, E.L. (1973). Devonian carrier shells (Euomphalidae) from North America and Germany. *United States Geological Survey Professional Paper* 824: 1–26
- Lloyd, D.G. (1970). The origin of the odour of the garlic snail *Oxychilus alliarius* (Müller) (Pulmonata: Zonitidae). *Proceedings of the Malacological Society of London* 39: 169–174
- Ludbrook, N.H. (1978). Quaternary molluscs of the western part of the Eucla Basin. *Bulletin of the Geological Survey of Western Australia* 125: 1–286
- Ludbrook, N.H. (1984). Quaternary molluscs of South Australia. *South Australian Department of Mines & Energy Handbook* 9: 1–327
- MacClintock, D. (1967). Shell structure of patelloid and bellerophonoid gastropods (Mollusca). *Bulletin of the Peabody Museum of Natural History* 22: 1–140
- Mackay, D.A. & Underwood, A.J. (1977). Experimental studies on homing in the intertidal patellid limpet *Cellana tramoserica* (Sowerby). *Oecologia* 30: 215–238
- Macpherson, J.H. & Gabriel, C.J. (1962). *Marine Molluscs of Victoria*. Melbourne University Press : Melbourne xv 475 pp.
- Marsh, H. (1977). The radular apparatus of *Conus*. *Journal of Molluscan Studies* 43: 1–11
- Marsh, L.M. (1976). Western Australian Asteroidea since H.L. Clark. *Thalassia Yugoslavia* 12: 213–225
- Marshall, B.A. (1983). A revision of the Recent Triphoridae of southern Australia. *Records of the Australian Museum, Supplement* 2: 1–119
- Marshall, D.J., Hodgson, A.N. & Trueman, E.R. (1989). The muscular hydrostat of a limpet tentacle. *Journal of Molluscan Studies* 55: 421–422
- Martin, A.W. (1983). Excretion. Pp. 353–405 in Saleuddin, A.S.M. & Wilbur, K.M. (eds) *The Mollusca. Vol. 5. Physiology. Pt 2*. Academic Press : New York
- May, W.L. (1923). *An Illustrated Index of Tasmanian Shells: with 47 plates and 1052 species*. John Vail : Hobart 99 pp.
- May, W.L. & Macpherson, J.H. (1958). *An Illustrated Index of Tasmanian Shells*. Government Printer : Hobart 72 pp.
- McLean, J.H. (1981). The Galapagos rift limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. *Malacologia* 21: 291–336
- McLean, J.H. (1988a). New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea. I. Systematic descriptions. *Philosophical Transactions of the Royal Society of London, Series B* 318: 1–32
- McLean, J.H. (1988b). New archaeogastropod limpet families in the hydrothermal vent community. *Malacological Review, Supplement* 5: 85–87
- McLean, J.H. (1989a). New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. *Zoologica Scripta* 18: 49–66
- McLean, J.H. (1989b). New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 1. Systematic descriptions and comparisons based on shell and radula characters. *Contributions in Science, Los Angeles County Museum* 407: 1–29
- McLean, J.H. (1990a). Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. *Journal of Zoology, London* 222: 485–528
- McLean, J.H. (1990b). A new genus and species of neomphalid limpet from the Mariana Vents and a review of current understanding of relationships among Neomphalacea and Peltospiracea. *The Nautilus* 104: 77–86
- McMahon, R.F. (1983). Physiological ecology of freshwater pulmonates. Pp. 359–430 in Russell-Hunter, W.D. (ed.) *The Mollusca. Vol. 6. Ecology*. Academic Press : New York
- McMichael, D.F. & Hiscock, L.D. (1958). A monograph of the freshwater mussels of Australasia. *Australian Journal of Marine and Freshwater Research* 9: 372–508
- McMichael, D.F. & Iredale, T. (1959). The land and freshwater Mollusca of Australia. Pp. 224–244 in Keast, A., Crocker, R.L. & Christian, C.S. (eds) *Biogeography and Ecology in Australia. Monographie Biologiae* 4. Junk : Den Haag
- McNair, C.G., Kier, W.M., La Croix, P.D. & Linsley, R.M. (1981). The functional significance of aperture form in gastropods. *Lethaia* 14: 63–70
- Menke, C.T. (1843). *Molluscorum Novae Hollandiae specimen, quod ... praeftuit ... J.G.C. Lehmann*. Libreria Aulica Hahniana : Hanover 46 pp.
- Miller, B.A. (1975). The biology of *Terebra gouldi* Deshayes, 1859, and a discussion of life history similarities among other terebrids of similar proboscis type. *Pacific Science* 29: 227–241
- Miller, B.A. (1979). The biology of *Hastula inconstans* (Hinds, 1844) and a discussion of life history similarities among other *Hastulas* of similar proboscis type. *Pacific Science* 33: 289–306
- Miller, S.L. (1974). Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* 14: 99–156
- Mordan, P.B. (1977). Factors affecting the distribution and abundance of *Aegopinella* and *Nesovitrea* (Pulmonata: Zonitidae) at Monds Wood National Nature Reserve, Huntingdonshire. *Biological Journal of the Linnean Society* 9: 59–72
- Morris, M.C. (1950). Dilation of the foot in *Uber (Polinices) strangei* (Mollusca, Class Gastropoda). *Proceedings of the Linnean Society of New South Wales* 75: 70–80
- Morris, T.E. & Hickman, C.S. (1981). A method for artificially protruding gastropod radulae and a new model of radular function. *The Veliger* 24: 85–90
- Morton, J.E. (1955a). The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proceedings of the Zoological Society of London* 125: 127–168
- Morton, J.E. (1955b). The functional morphology of the British Ellobiidae (Gastropoda, Pulmonata) with special reference to the digestive and reproductive systems. *Philosophical Transactions of the Royal Society, Series B* 239: 89–160

14. CLASS GASTROPODA

- Morton, J.E. (1965). Form and function in the evolution of the Vermetidae. *Bulletin of the British Museum (Natural History) Zoology* 11: 585–630
- Morton, J.E. (1979). *Molluscs*. Hutchinson : London 5th edn 264 pp.
- Morton, J.E. & Yonge, C.M. (1964). Classification and structure of the Mollusca. Pp. 1–58 in Wilbur, K.M. & Yonge, C.M. (eds) *The Physiology of the Mollusca*. Vol. 1. Academic Press : New York
- Mpitsos, G.J. & Davis, D.T. (1973). Learning: classical and avoidance conditioning in the mollusk *Pleurobranchaea*. *Science* 180: 317–320
- Mpitsos, G.J. & Lukowich, K. (1985). Learning in gastropod molluscs. Pp. 95–267 in Willows, A.D. (ed.) *The Mollusca*. Vol. 8. *Neurobiology and Behavior*. Pt 1. Academic Press : New York
- Murray, M.J. & Lewis, E.R. (1974). Sensory control of prey capture in *Navanax inermis*. *The Veliger* 17: 156–158
- Nybakken, J. & McDonald, G. (1981). Feeding mechanisms of West American nudibranchs feeding on Bryozoa, Cnidaria and Ascidiacea, with special respect to the radula. *Malacologia* 20: 439–449
- Orton, J.H. (1929). Observations on *Patella vulgata*. Part 3. Habitat and habits. *Journal of the Marine Biological Association of the United Kingdom* 16: 277–288
- Owen, G. (1966a). Feeding. Pp. 1–52 in Wilbur, K.M. & Yonge, C.M. (eds) *Physiology of Mollusca*. Vol. 2. Academic Press : New York
- Owen, G. (1966b). Digestion. Pp. 53–96 in Wilbur, K.M. & Yonge, C.M. (eds) *Physiology of Mollusca*. Vol. 2. Academic Press : New York
- Palmer, A.R. (1977). Function of shell sculpture in marine gastropods: hydrodynamic destabilization in *Ceratosoma foliatum*. *Science* 197: 1293–1295
- Palmer, A.R. (1979). Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 33: 697–713
- Pennington, J.T. & Chia, F.-S. (1985). Gastropod torsion: a test of Garstang's hypothesis. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 169: 391–396
- Pilsbry, H.A. (1948). *Land Mollusca of North America (north of Mexico)*. Academy of Natural Science Philadelphia Monograph No. 3 2(2): 521–1113
- Ponder, W.F. (1968). The morphology of some small New Zealand prosobranchs. *Records of the Dominion Museum* 6: 61–95
- Ponder, W.F. (1970). Some aspects of the morphology of four species of the neogastropod family Marginellidae with a discussion on the evolution of the toxoglossan poison gland. *Journal of the Malacological Society of Australia* 2: 55–81
- Ponder, W.F. (1972). The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Neogastropoda). *Malacologia* 11: 295–342
- Ponder, W.F. (1973). The origin and evolution of the Neogastropoda. *Malacologia* 12: 295–338
- Ponder, W.F. (1978). The unfigured Mollusca of J. Thiele. 1930 published in Die Fauna Sudwest-Australiens. *Records of the Western Australian Museum* 6: 423–441
- Ponder, W.F. (1983a). Review of the genera of Barleeidae (Mollusca: Gastropoda: Rissoacea). *Records of the Australian Museum* 35: 231–281
- Ponder, W.F. (1983b). A revision of the recent Xenophoridae of the world and of the Australian fossil species. *Memoirs of the Australian Museum* 17: 1–126
- Ponder, W.F. (1984). A review of the genera of the Iravadiidae (Mollusca: Gastropoda: Rissoacea) with an assessment of the relationships of the family. *Malacologia* 25: 21–71
- Ponder, W.F. (1985). A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Records of the Australian Museum Supplement* 4: 1–221
- Ponder, W.F. (1986). Glacidorbidae (Glacidorbacea: Basommato-phora), a new family and superfamily of operculate freshwater gastropods. *Zoological Journal of the Linnean Society* 87: 53–83
- Ponder, W.F. (1988b). The truncatelloidean (=rissoacean) radiation – a preliminary phylogeny. *Malacological Review, Supplement* 4: 129–166
- Ponder, W.F. (1992). A new genus and species of aquatic cave-living snail from Tasmania (Mollusca: Gastropoda: Hydrobiidae). *Proceedings of the Royal Society of Tasmania* 126: 23–28
- Ponder, W.F. (1994). Australian freshwater Mollusca: conservation priorities and indicator species. *Memoirs of the Queensland Museum* 36: 191–196
- Ponder, W.F. & Clark, G.A. (1990). A radiation of hydrobiid snails in threatened artesian springs in western Queensland. *Records of the Australian Museum* 42: 301–363
- Ponder, W.F., Clark, G.A., Miller, A.C. & Toluzzi, A. (1993). On a major radiation of freshwater snails in Tasmania and eastern Victoria: a preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). *Invertebrate Taxonomy* 7: 501–750
- Ponder, W.F., Colgan, D.J., Clark, G.A., Miller, A.C. & Terzis, T. (1994). Microgeographic, genetic and morphological differentiation of freshwater snails - the Hydrobiidae of Wilsons Promontory, Victoria, south-eastern Australia. *Australian Journal of Zoology* 42: 557–678
- Ponder, W.F. & Creese, R.A. (1980). A revision of the Australian species of *Notoacmea*, *Collisella* and *Patelloida* (Mollusca: Gastropoda: Acmaeidae). *Journal of the Malacological Society of Australia* 4: 167–208
- Ponder, W.F. & Gooding, R.U. (1978). Four new eulimid gastropods associated with shallow-water diadematid echinoids in the western Pacific. *Pacific Science* 32: 157–181
- Ponder, W.F., Hershler, R. & Jenkins, B. (1989). An endemic radiation of hydrobiid snails from artesian springs in northern South Australia: their taxonomy, physiology, distribution and anatomy. *Malacologia* 31: 1–140
- Ponder, W.F. & Lindberg, D.R. (1996). Gastropod phylogeny – challenges for the 90s. Pp. 135–154 in Taylor, J.D. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Ponder, W.F. & Lindberg, D.R. (1997). Towards a phylogeny of gastropod molluscs – an analysis using morphological characters. *Zoological Journal of the Linnean Society* 19: 83–265
- Ponder, W.F. & Taylor, J.D. (1992). Predatory shell drilling by two species of *Austroginella* (Gastropoda: Marginellidae). *Journal of Zoology, London* 228: 317–328
- Ponder, W.F. & Vokes, E.H. (1988). A revision of the Indo-west Pacific fossil and Recent species of *Murex* s.s. and *Haustellum* (Mollusca: Gastropoda: Muricidae). *Records of the Australian Museum, Supplement* 8: 1–160
- Ponder, W.F. & Warén, A. (1988). Classification of the Caenogastropoda and Heterostropho – a list of the family-group names and higher taxa. Pp. 288–328 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement* 4
- Ponder, W.F. & Yoo, E.K. (1976). A revision of the Australian and tropical Indo-Pacific Tertiary and Recent species of *Pisinna* (=Estea) (Mollusca: Gastropoda: Rissoacea). *Records of the Australian Museum* 30: 150–247
- Ponder, W.F. & Yoo, E.K. (1980). A review of the genera of the Cingulopsidae with a revision of the Australian and tropical Indo-Pacific species (Mollusca: Gastropoda: Prosobranchia). *Records of the Australian Museum* 33: 1–88
- Powell, A.W.B. (1979). *New Zealand Mollusca, Marine, Land and Freshwater Shells*. Collins : Auckland xiv 500 pp.
- Preston, R.J. & Lee, R.M. (1973). Feeding and behavior in *Aplysia californica*: role of chemical and tactile stimuli. *Journal of Comparative Physiology and Psychology* 82: 361–381
- Prince, J.D., Sellers, T.L., Ford, W.B. & Talbot, S.R. (1987). Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*: Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 106: 243–263
- Purchon, R.D. (1968). *The Biology of the Mollusca*. Pergamon Press : Oxford xxv 560 pp.

- Quoy, J.R.C. & Gaimard, J.P. (1830–1834). *Voyages de decouvertes de l'Astrolabe execute par ordre du Roi pendant les années 1826–1827–1828–1829 sous le commandement de M.J. Dumont d'Urville*. Zoologie. J. Tastu : Paris, 4 vols, 1 268 pp., 686 pp., 945 pp., 390 pp., atlas 198 pp.
- Raup, D.M. (1961). The geometry of coiling in gastropods. *Proceedings of the National Academy of Science* 47: 602–609
- Raup, D.M. (1966). Geometric analysis of shell coiling: general problems. *Journal of Paleontology* 40: 1178–1190
- Rees, W.J. (1964). A review of the breathing devices in land operculate snails. *Proceedings of the Malacological Society of London* 36: 55–67
- Rigby, J.E. (1963). Alimentary and reproductive systems of *Oxychilus cellarius* (Müller) (Stylommatophora). *Proceedings of the Zoological Society of London* 141: 311–359
- Rippingale, O.H. & McMichael, D.F. (1961). *Queensland and Great Barrier Reef Shells*. Jacaranda Press : Brisbane 210 pp.
- Robertson, R. (1970). Systematics of Indo-Pacific *Philippia* (*Psilaxis*), architectonicid gastropods with eggs and young in the umbilicus. *Pacific Science* 24: 66–83
- Robertson, R. (1985). Four characters and the higher category systematics of gastropods. *Bulletin of the American Malacological Union. Special Edition* 1: 1–22
- Robertson, R. (1989). Spermatophores of aquatic non-stylommatophoran gastropods: a review with new data on *Heliacus* (Architectonicidae). *Malacologia* 30: 341–364
- Rose, R.A. (1985). The spawn and development of twenty-nine New South Wales opisthobranchs. *Proceedings of the Linnean Society of New South Wales* 108: 23–36
- Rosewater, J. (1970). The family Littorinidae in the Indo-Pacific. Part 1. The subfamily Littorininae. *Indo-Pacific Mollusca* 2: 417–506
- Rudman, W.B. (1971a). Structure and function of the gut in the Bullomorpha (Opisthobranchia) Part 1. Herbivores. *Journal of Natural History* 5: 647–675
- Rudman, W.B. (1971b). On the opisthobranch genus *Haminoea* Turton Kingston. *Pacific Science* 25: 545–559
- Rudman, W.B. (1972a). The anatomy of the opisthobranch genus *Hydatina* and the functioning of the mantle cavity and alimentary canal. *Zoological Journal of the Linnean Society* 51: 121–139
- Rudman, W.B. (1972b). A comparative study of the genus *Philinopsis* Pease, 1860 (Aglajidae: Opisthobranchia). *Pacific Science* 26: 381–399
- Rudman, W.B. (1981a). Further studies on the anatomy and ecology of opisthobranch molluscs feeding on the scleractinian coral *Porites*. *Zoological Journal of the Linnean Society* 71: 373–412
- Rudman, W.B. (1981b). The anatomy and biology of alcyonarian-feeding aeolid opisthobranch molluscs and their development of symbiosis with zooxanthellae. *Zoological Journal of the Linnean Society* 72: 219–262
- Rudman, W.B. (1981c). Polyp mimicry in a new species of aeolid nudibranch mollusc. *Journal of Zoology, London* 193: 421–427
- Rudman, W.B. (1982). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris quadricolor*, *C. lineolata* and *Hypselodoris nigrolineata* colour groups. *Zoological Journal of the Linnean Society* 76: 183–241
- Rudman, W.B. (1983). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris splendida*, *C. aspersa* and *Hypselodoris placida* colour groups. *Zoological Journal of the Linnean Society* 78: 105–173
- Rudman, W.B. (1984). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. *Zoological Journal of the Linnean Society* 81: 115–273
- Rudman, W.B. (1985). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris aureomarginata*, *C. verrieri* and *C. fidelis* colour groups. *Zoological Journal of the Linnean Society* 83: 241–299
- Rudman, W.B. (1986a). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: the genus *Glossodoris* Ehrenbergh (= *Casella*, H. & A. Adams). *Zoological Journal of the Linnean Society* 86: 101–184
- Rudman, W.B. (1986b). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Noumea purpurea* and *Chromodoris decora* colour groups. *Zoological Journal of the Linnean Society* 86: 309–353
- Rudman, W.B. (1986c). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Noumea flava* colour group. *Zoological Journal of the Linnean Society* 86: 377–404
- Rudman, W.B. (1987a). The genus *Trapania* (Nudibranchia: Goniodorididae) in the Indo-West Pacific. *Journal of Molluscan Studies* 53: 189–212
- Rudman, W.B. (1987b). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris epicuria*, *C. aureopurpurea*, *C. annulata*, *C. coi* and *Risbecia tryoni* colour groups. *Zoological Journal of the Linnean Society* 90: 305–407
- Rudman, W.B. (1988). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: the genus *Ceratosoma* J.E. Gray. *Zoological Journal of the Linnean Society* 93: 133–185
- Rudman, W.B. (1991). Purpose in pattern: the evolution of colour in chromodorid nudibranchs. *Journal of Molluscan Studies* 57: 5–21
- Rudman, W.B. & Avern, G.J. (1989). The genus *Rostanga* Bergh, 1879 (Nudibranchia: Dorididae) in the Indo-West Pacific. *Zoological Journal of the Linnean Society* 96: 281–338
- Runham, N.W. (1969). The use of the scanning electron microscope in the study of the gastropod radula: the radulae of *Agriolimax reticulata* and *Nucella lapillus*. Pp. 179–185 in Paget, O.E. (ed.) *Proceedings of the Third European Malacological Congress, Vienna 1968*. *Malacologia* 9
- Runham, N.W. (1975). Alimentary canal. Pp. 53–104 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional Anatomy and Physiology*. Academic Press : New York
- Runham, N.W. & Hunter, P.J. (1970). *Terrestrial Slugs*. Hutchinson University Library : London 184 pp.
- Runnegar, B. (1981). Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs. *Lethaia* 14: 311–322
- Russell-Hunter, W.D. (1978). Ecology of freshwater pulmonates. Pp. 335–384 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 2A. Systematics, Evolution and Ecology*. Academic Press : New York
- Russell-Hunter, W.D. (1979). *The Life of Invertebrates*. Macmillan : New York xi 650 pp.
- Russell-Hunter, W.D. & Russell-Hunter, M. (1968). Pedal expansion in the naticid snails. I. Introduction and weighing experiments. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 135: 548–562
- Salvini-Plawen, L.v. (1980). A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* 19: 249–278
- Salvini-Plawen, L.v. (1981). On the origin and evolution of the Mollusca. in *Origine dei Grande Phyla dei Metazoi. Atti dei convegni Lincei (Roma)* 49: 235–293
- Salvini-Plawen, L.v. (1985). Early evolution and the primitive groups. Pp. 59–150 in Trueman, E.R. & Clarke M.R. (eds) *The Mollusca. Vol. 10. Evolution*. Academic Press : Orlando
- Salvini-Plawen, L.v. (1988). The structure and function of molluscan digestive systems. Pp. 301–379 in Trueman, E.R. & Clarke M.R. (eds) *The Mollusca. Vol. 11. Form and Function*. Academic Press : Orlando
- Salvini-Plawen, L.v. (1990). Origin, phylogeny and classification of the phylum Mollusca. *Iberus* 9: 1–33
- Salvini-Plawen, L.v. & Haszprunar, G. (1987). The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *Journal of Zoology, London* 211: 747–770
- Scheltema, R.S. (1971). Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 140: 284–322
- Scheltema, R.S. (1978). On the relationship between dispersal of pelagic veliger larvae and the evolution of marine prosobranch gastropods. Pp. 303–322 in Battaglia, B. & Beardmore, J. (eds) *Marine Organisms*. Plenum Publishing : New York

14. CLASS GASTROPODA

- Scheltema, R.S. & Williams, I.P. (1983). Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and western Pacific mollusks. *Bulletin of Marine Science* 33: 545–565
- Schulte, G.R. & Scheuer, P.J. (1982). Defensive allomones of some marine molluscs. *Tetrahedron* 38: 1857–1863
- Shepherd, S.A. & Laws, H.M. (1974). Studies on southern Australian abalone. II. Reproduction of five species. *Australian Journal of Marine and Freshwater Research* 25: 49–62
- Shimek, R.L. & Kohn, A.J. (1981). Functional morphology and evolution of the toxoglossan radula. *Malacologia* 20: 423–438
- Short, J.W. & Potter, P.G. (1987). *Shells of Queensland and the Great Barrier Reef*. R.A. Brown Associates : Bathurst vi 134 pp.
- Signor, P.W. III (1983). Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. *Malacologia* 23: 313–320
- Signor, P.W. III & Kat, P.W. (1984). Functional significance of columellar folds in turritelliform gastropods. *Journal of Paleontology* 58: 210–216
- Singer, C. (1950). *A History of Biology*. Henry Schuman : New York xxv 579 pp.
- Singleton, F.A. (1941). The Tertiary geology of Australia. *Proceedings of the Royal Society of Victoria* 53: 1–125
- Singleton, F.A. (1945). A catalogue of type and figured specimens of fossils in the Melbourne University Geology Department. *Proceedings of the Royal Society of Victoria* 56: 229–284
- Smith, B.J. (1971). Carnivorous snails of the family Paryphantidae. *Australian Natural History* 17: 55–58
- Smith, B.J. (1992). Non-Marine Mollusca. In Houston, W.W.K. (ed.) *Zoological Catalogue Vol. 8*. Australian Government Publishing Service : Canberra xii 405 pp.
- Smith, B.J. & Black, J.H. (1969). Biographies, combined bibliography and new names list of John Henry Gatliff (1848–1935) and Charles John Gabriel (1879–1963). *Journal of the Malacological Society of Australia* 12: 32–47
- Smith, B.J. & Kershaw, R.C. (1979). *Field Guide to the Non-marine Molluscs of South Eastern Australia*. Australian National University Press : Canberra x 285 pp.
- Smith, B.J. & Kershaw, R.C. (1981). *Tasmanian Land and Freshwater Molluscs*. University of Tasmania Press : Hobart 148 pp.
- Smith, E.H. (1967). The neogastropod stomach, with notes on the digestive diverticula and intestine. *Transactions of the Royal Society of Edinburgh* 67: 4–41
- Smith, F.G.W. (1935). The development of *Patella vulgata*. *Philosophical Transactions of the Royal Society, Series B* 225: 95–125
- Solem, A.G. (1988). Maximum in the minimum. Biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia* 9: 59–113
- Solem, A.G. (1972a). Malacological applications of scanning electron microscopy – II. Radular structure and functioning. *The Veliger* 14: 327–336
- Solem, A.G. (1972b). Microarmature and barriers in the aperture of land snails. *The Veliger* 15: 81–87
- Solem, A.G. (1974a). *The Shell Makers*. John Wiley & Sons : New York xii 289 pp.
- Solem, A.G. (1974b). Patterns of radular tooth structure in carnivorous land snails. *The Veliger* 17: 81–88
- Solem, A.G. (1978). Classification of the land Mollusca. Pp. 49–97 in Fretter, V. & Peake, J. (eds) *Pulmonates*. Vol. 2A. *Systematics, Evolution and Ecology*. Academic Press : New York
- Solem, A.G. (1979). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). I. Taxa with trans-Australian distribution. *Records of the Western Australian Museum, Supplement* 10: 5–142
- Solem, A.G. (1981a). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale, 1933. *Records of the Western Australian Museum, Supplement* 11: 147–320
- Solem, A.G. (1981b). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from the Ningbing Ranges and nearby areas. *Records of the Western Australian Museum, Supplement* 11: 321–425
- Solem, A.G. (1981c). Small land snails from northern Australia, 1: species of *Gyliotrachela* Tomlin, 1930 (Mollusca: Pulmonata: Vertiginidae). *Journal of the Malacological Society of Australia* 5: 87–100
- Solem, A.G. (1984). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale, 1933 and related genera. *Records of the Western Australian Museum, Supplement* 17: 427–705
- Solem, A.G. (1985). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining genera and addenda to the Kimberley. *Records of the Western Australian Museum, Supplement* 20: 707–981
- Solem, A.G. (1986). Pupilloid land snails from the south and mid-west coasts of Australia. *Journal of the Malacological Society of Australia* 7: 95–124
- Solem, A.G., Tillier, S. & Mordan, P. (1984). Pseudo-operculate pulmonate land snails from New Caledonia. *The Veliger* 27: 193–199
- Spengel, J.W. (1881). Die Geruchsorgane und das Nervensystem der Mollusken. *Zeitschrift für Wissenschaftliche Zoologie* 35: 332–384
- Stanisic, J. (1987). Studies on the Charopidae of tropical and subtropical Australia. I. *Oreokera*: a primitive genus from the high mountains of North Queensland (Mollusca: Pulmonata: Charopidae). *Journal of the Malacological Society of Australia* 8: 1–21
- Stanisic, J. (1990). Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* 30: 1–241
- Stanisic, J. (1994). The distribution and patterns of species diversity of land snails in eastern Australia. *Memoirs of the Queensland Museum* 36: 207–214
- Stoddart, J.A. (1985). Analysis of species lineages of some Australian thiarids (Thiaridae, Prosobranchia, Gastropoda) using the evolutionary species concept. *Journal of the Malacological Society of Australia* 7: 7–16
- Strzelecki, P.E. de. (1845). *Physical description of New South Wales and Van Dieman's Land accompanied by a geological map, section, and diagrams, and figures of the organic remains*. Longman, Brown, Green & Longmans : London 462 pp.
- Tardy, J. (1991). Types of opisthobranch veligers: their notum formation and torsion. *Journal of Molluscan Studies* 57: 103–112
- Tassell, C.B. (1976). A revision of the gastropod fauna of the Lilydale limestone (early Devonian) of Victoria. *Memoirs of the National Museum of Victoria* 37: 1–21
- Tassell, C.B. (1977). Gastropods from some Early Devonian limestones of the Walhalla Synclinorium, Central Victoria. *Memoirs of the National Museum of Victoria* 38: 231–246
- Tassell, C.B. (1978). Gastropods from the early Devonian Bell Point Limestone. Cape Liptrap Rennaeta, Victoria. *Memoirs of the National Museum of Victoria* 39: 19–32
- Tate, R. (1887). On the influence of physiographic changes in the distributions of life in Australia. *Reports of the Australasian Association for the Advancement of Science* 1: 312–325
- Tate, R. (1894). Unrecorded genera of the older Tertiary fauna of Australia, including diagnoses of some new genera and species. *Journal of the Royal Society of New South Wales* 27: 167–196
- Taylor, D.W. & Sohl, N.F. (1962). An outline of gastropod classification. *Malacologia* 1: 7–32
- Taylor, J.D. (1981). The evolution of predators in the late Cretaceous and their ecological significance. Pp. 229–240 in Greenwood, P.H. (ed.) *The Evolving Biosphere*. British Museum (Natural History) and Cambridge University Press : London
- Taylor, J.D. & Miller, J.A. (1989). The morphology of the osphradium in relation to feeding habits in meso- and neogastropods. *Journal of Molluscan Studies* 55: 227–237

- Taylor, J.D., Morris, N.J. & Taylor, C.N. (1980). Food specialisation and the evolution of predatory prosobranch gastropods. *Palaeontology* 23: 375–409
- Thiele, J. (1929–1931). *Handbuch der Systematischen Weichtierkunde*. Bd 1. G. Fischer : Jena vi 778 pp.
- Thiele, J. (1930). Gastropoda und Bivalvia. Pp. 559–596 in *Michaelsen, W. Die Fauna Südwest-Australiens. Ergebnisse der Hamburger Südwest-Australischen Forschungreise 1905, herausgegeben von ... W. Michaelsen und ... R. Hartmeyer*. Jena 5 vols
- Thompson, T.E. (1958). The natural history, embryology, larval biology and post-larval development of *Adalaria proxima* (Alder & Hancock) (Gastropoda: Opisthobranchia). *Philosophical Transactions of the Royal Society, Series B* 242: 1–58
- Thompson, T.E. (1976). *Biology of Opisthobranch Molluscs*. Vol. 1. Ray Society Publication No. 156 : London 207 pp.
- Thompson, T.E. (1986). Investigation of the acidic allomone of the gastropod mollusc *Philine aperta* by means of ion chromatography and histochemical localisation of sulphate and chloride ions. *Journal of Molluscan Studies* 52: 38–44
- Thorson, G. (1961). Length of pelagic life in marine invertebrates as related to larval transport by ocean currents. Pp. 455–474 in *Sears, M. (ed.) Oceanography*. American Association for the Advancement of Science Publication 67 : Washington
- Tomba, A.S. (1984). Land snails (Stylommatophora). Pp. 47–140 in *Tomba, A.S., Verdonk, N.H. & van den Biggelaar, J.A.M. (eds) The Mollusca. Vol. 7. Reproduction*. Academic Press : New York
- Troschel, F.H. (& Thiele, J.) (1856–1893). *Das Gebiss der Schnecken, zur Begründung einer Natürlichen Classification*. Nicoläische Verlagsbuchhandlung : Berlin 2 vols, 252 pp, 409 pp. [Pts 1–6 (1856–1879); Pts 7 & 8 (1891–1893) by J. Thiele, written after Troschel's death]
- Trueman, E.R. & Brown, A.C. (1989). The effect of shell shape on the burrowing performance of the species of *Bullia* (Gastropoda: Nassariidae). *Journal of Molluscan Studies* 55: 129–131
- Trueman, E.R. & Brown, A.C. (1993). Evolution of burrowing in gastropods: the behaviour of the rocky-shore whelk *Burnupena catarrhacta* on sand. *Journal of Molluscan Studies* 59: 261–263
- Underwood, A.J. (1974). The reproductive cycles and geographic distribution of some common eastern Australian prosobranchs (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 25: 63–88
- Underwood, A.J. (1977). Movements of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* 26: 191–201
- Underwood, A.J. (1979). The ecology of intertidal gastropods. *Advances in Marine Biology* 16: 111–210
- Verdonk, N.H. & van den Biggelaar, J.A.M. (1983). Early development and formation of the germ layers. Pp. 91–122 in *Verdonk, N.H., van den Biggelaar, J.A.M. & Tomba, A.S. (eds) The Mollusca. Vol. 3. Development*. Academic Press : New York
- Vermeij, G.J. (1970). Adaptive versatility and skeleton construction. *American Naturalist* 104: 253–260
- Vermeij, G.J. (1971a). Gastropod evolution and morphological diversity in relation to shell geometry. *Journal of Zoology, London* 163: 15–23
- Vermeij, G.J. (1971b). The geometry of shell sculpture. *Forma et Functio* 4: 319–325
- Vermeij, G.J. (1975). Marine faunal dominance and molluscan shell form. *Evolution* 28: 656–664
- Vermeij, G.J. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3: 245–258
- Vermeij, G.J. (1978a). Adaptive versatility and skeleton construction. *American Naturalist* 104: 253–260
- Vermeij, G.J. (1978b). *Biogeography and Adaptation*. Harvard University Press : Cambridge xi 332 pp.
- Vermeij, G.J. (1979). Shell architecture and causes of death of Micronesian reef snails. *Evolution* 33: 686–696
- Vermeij, G.J. (1988). *Evolution and escalation. An ecological history of life*. Princeton University Press : Princeton, New Jersey xv 527 pp.
- Vermeij, G.J. & Zipser, E. (1986). Burrowing performance in some tropical Pacific gastropods. *The Veliger* 29: 200–206
- Voltzow, J. (1987). Torsion reexamined: the timing of the twist. *American Zoologist* 27: 84A (abstract)
- Voltzow, J. (1994). Gastropoda: Prosobranchia. Pp. 111–252 in *Harrison, F.W. & Kohn, A.J. (eds) Microscopic Anatomy of Invertebrates. Vol. 5. Mollusca I*. Wiley-Liss : New York
- Walker, G. (1972). The digestive gland of the slug *Ariolimax reticulatus* (Müller): experiments on phagocytosis and nutrient absorption. *Proceedings of the Malacological Society of London* 40: 33–43
- Ward, J. (1965). The digestive tract and its relation to feeding habits in the stenoglossan prosobranch *Coralliophila abbreviata* (Lamarck). *Canadian Journal of Zoology* 43: 447–464
- Warén, A. & Bouchet, P. (1989). New gastropods from East Pacific hydrothermal vents. *Zoologica Scripta* 18: 67–102
- Warén, A. & Ponder, W.F. (1991). New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). *Zoologica Scripta* 20: 27–56
- Watabe, N. (1988). Shell structure. Pp. 691–104 in *Trueman, E.R. & Clarke, M.R. (eds) The Mollusca. Vol. 11. Form and Function*. Academic Press : New York
- Webber, H.H. (1977). Gastropoda: Prosobranchia. Pp. 1–97 in *Giese, A.C. & Pearse, J.S. (eds) Reproduction in Marine Invertebrates. Vol. 4. Molluscs: Gastropods and Cephalopods*. Academic Press : New York
- Weiner, S. & Hood, L. (1975). Soluble protein of the organic matrix of mollusk shells a potential template for shell formation. *Science* 190: 987–989
- Wells, F.E. (1970). An ecological study of two sympatric species of *Fasciolaria* (Mollusca: Gastropoda) in Alligator Harbor, Florida. *The Veliger* 13: 95–108
- Wells, F.E. (1980). The distribution of shallow-water marine prosobranch gastropod molluscs along the coastline of Western Australia. *The Veliger* 22: 232–247
- Wells, F.E. (1986). A redescription of the sea hare *Aplysia gigantea* Sowerby 1869. *Journal of the Malacological Society of Australia* 7: 173–178
- Wells, F.E. (1989). Holoplanktonic molluscs (class Gastropoda). Pp. 823–840 in *Shepherd, S.A. & Thomas, I.M. (eds) The Marine Invertebrates of Southern Australia. Vol. 2. Handbooks of the Flora and Fauna of South Australia*. Government Printer : Adelaide
- Wells, F.E. & Bryce, C.W. (1986). *Seashells of Western Australia*. Western Australian Museum : Perth 207 pp.
- Wells, F.E. & Kilburn, R.N. (1986). Three temperate water species of South African gastropods recorded for the first time in southwestern Australia. *The Veliger* 28: 453–456
- Wells, F.E. & Lalli, C.M. (1977). Reproduction and brood protection in the Caribbean gastropods *Coralliophila abbreviata* (Lamarck) and *C. caribaea*. *Journal of Molluscan Studies* 43: 79–87
- Whitley, G.P. (1947). The fluvifaunulae of Australia with particular reference to freshwater fishes in Western Australia. *Western Australian Naturalist* 1: 49–53
- Whitley, G.P. (1968). Joyce Allan (1896–1966). Obituary, Bibliography and Index of her new scientific names. *Journal of the Malacological Society of Australia* 1(11): 59–61
- Whitley, G.P. (1970). *Early History of Australian Zoology*. Royal Zoological Society of New South Wales : Sydney 75 pp.
- Whitley, G.P. & Ponder, W.F. (1973). Obituary. Tom Iredale. (1880–1972). *Journal of the Malacological Society of Australia* 2: 361–364
- Wilbur, K.M. & Saleuddin, A.S.M. (1983). Shell formation. Pp. 235–287 in *Saleuddin & Wilbur, K.M. (eds) The Mollusca. Vol. 4. Physiology. Pt 1*. Academic Press : New York

14. CLASS GASTROPODA

- Willan, R.C. (1987). Phylogenetic systematics and zoogeography of Australian nudibranchs. 1. The presence of the aeolid *Godiva quadricolor* (Barnard) in Western Australia. *Journal of the Malacological Society of Australia* 7: 71-85
- Willan, R.C. & Coleman, N. (1984). *Nudibranchs of Australasia*. Australasian Marine Photographic Index : Caringbah, New South Wales 56 pp.
- Wilson, B.R. (1993). *Australian marine Shells. Prosobranch Gastropods, Part 1*. Odyssey Publishing : Kallaroo, Western Australia 408 pp.
- Wilson, B.R. (1994). *Australian marine Shells. Prosobranch Gastropods, Part 2 (Neogastropods)*. Odyssey Publishing : Kallaroo, Western Australia 370 pp.
- Wilson, B.R. & Allen, G.R. (1987). Major components and distribution of marine fauna. Pp. 43-68 in Dyne, G.R. & Walton, D.W. (eds) *Fauna of Australia. Vol. 1A. General Articles*. Australian Government Publishing Service : Canberra
- Wilson, B.R. & Gillett, K. (1971). *Australian Shells*. Reed : Sydney 168 pp.
- Wilson, D.P. & Wilson, M.A. (1956). A contribution to the biology of *Ianthina janthina* (L.). *Journal of the Marine Biological Association of the United Kingdom* 35: 291-305
- Wingstrand, K.G. (1985). On the anatomy and relationships of Recent Monoplacophora. *Galathea Report* 16: 7-94
- Woollacott, M.H. (1974). Patterned neural activity associated with prey capture in *Navanax* (Gastropoda: Aplysiacea). *Journal of Comparative Physiology* 94: 69-84
- Yonge, C.M. (1938). Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. *Journal of the Marine Biological Association of the United Kingdom* 22: 453-468
- Yonge, C.M. (1947). The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 232: 443-518
- Young, D.K. (1969a). The functional morphology of the feeding apparatus of some Indo-West Pacific dorid nudibranchs. *Malacologia* 9: 421-446
- Young, D.K. (1969b). *Okadaia elegans*, a tube-boring nudibranch mollusc from the central and West Pacific. *American Zoologist* 9: 903-907
- Zilch, A. (1959-1960). Gastropoda, Teil 2, Euthyneura. Pp. 401-834 in Schindewolf, O.H. (ed.) *Handbuch der Paläozoologie. Vol 6*. Borntraeger : Berlin
- Zipser, E. & Vermeij, G.G. (1978). Crushing behavior of tropical and temperate crabs. *Journal of Experimental Marine Biology and Ecology* 31: 155-172

PROSOBRANCHS

— CHAPTER 15 —

A GENERAL INTRODUCTION TO THE PATELLOGASTROPODA, COCCULINIFORM LIMPETS, VETIGASTROPODA, NERITOPSINA, CAENOGASTROPODA AND LOWER HETEROBRANCHS

INTRODUCTION

As outlined in Chapter 14, the traditional view of gastropod classification is of three main groups, each of which is given the rank of subclass: Prosobranchia, Opisthobranchia and Pulmonata. It is now realised that the Opisthobranchia, Pulmonata and a few groups previously included in Prosobranchia form a clade, Heterobranchia, whereas the remaining prosobranchs are paraphyletic (see Chapter 14; Haszprunar 1985d, 1988a, 1988b; Bieler 1992a; Ponder & Lindberg 1996, 19967). The traditional prosobranch group consists of four very distinct clades, the Patellogastropoda, Vetigastropoda, Neritopsina and Caenogastropoda, each of which should be considered as distinct as Heterobranchia. Relationships of another group, the Cocculiniformia, and also of some of the taxa associated with deep-sea vents, are problematical. Thus the term 'prosobranchs' as used here applies to an artificial grouping roughly equivalent to 'Streptoneura' as used by Haszprunar (1988a). A summary of the families and higher groups of 'prosobranchs' that occur in the Australian fauna is given in Table 15.1.

Many of the general aspects of 'prosobranchs' are covered in Chapter 14, but in this chapter the morphology and physiology of the major organ systems are reviewed in more detail and some of the evolutionary trends seen in the clades within the 'prosobranch' grouping are examined further. More comprehensive reviews can be found in Fretter & Graham (1962, 1994), Hyman (1967), Franc (1968) and Voltzow (1994).

Of the three traditionally recognised major groups of gastropods, the 'prosobranchs' form the largest. D.W. Taylor & Sohl (1962), in their outline of gastropod classification, enumerated over six thousand Recent gastropod genera and subgenera – about 54% prosobranchs, 37% pulmonates and 9% opisthobranchs, as then recognised. The 'prosobranchs' include the most primitive gastropods. The Heterobranchia were derived from an ancestor within this paraphyletic grouping. Impressive adaptive radiations have occurred within the taxa loosely grouped as 'prosobranchs', and their modern representatives show an astonishing diversity of morphological and physiological features.

As described in Chapter 14, torsion is a fundamental characteristic of gastropods. It is a larval phenomenon in which the visceral mass is rotated counter-clockwise 180° relative to the head-foot. The adaptive significance of torsion has been discussed by many workers and various theories have been advanced (see summaries in Haszprunar 1988a and Ponder & Lindberg 1997). As a consequence of torsion, the 'prosobranch' mantle cavity lies directly over the head and, internally, all structures which pass between the head, foot and visceral mass are affected. In the nervous system, this is expressed as streptoneury (from the Greek *streptos*, meaning *twisted* and hence the term 'streptoneuran gastropods'). The visceral loop twists so that the connective from the right pleural ganglion crosses to the left side over the oesophagus on its way to the visceral ganglia, whereas that from the left pleural ganglion passes to the right side beneath the oesophagus. Whereas streptoneury is usually clearly evident on

dissection, the effect of torsion on other systems is often not appreciated. The oesophagus twists in the region where the nerves cross it so that the mid-dorsal part curves round the left side to the ventral side, and the mid-ventral part twists up on the right to the dorsal side. The effects of torsion can also be easily seen in species in which the mid-dorsal part of the oesophagus differs from the lateral walls of the oesophagus in structure and colour. The anterior aorta leaves the heart which lies on the left and crosses the gut dorsally to occupy a ventral position anteriorly on the right.

In certain respects, the organisation of some members of the group now known as Vetigastropoda is the least modified in modern gastropods. This group comprises many of the families previously included in the Archaeogastropoda, another paraphyletic group. We briefly describe an hypothetical basal member of this group as a 'basic gastropod' and outline some of its anatomical features. This is followed by a brief description of each of the major organ systems, focusing on the trochid *Calliostoma zizyphinum*, a vetigastropod taken as a general example of 'prosobranch' organisation. Although this description is based on a European species, the genus occurs in Australia and is a member of a very large, diverse and ecologically important family of marine gastropods in this region. A brief account of how other 'prosobranchs' differ from *Calliostoma* is also given for each organ system.

Some vetigastropods have paired pallial organs, osphradia, ctenidia, auricles and kidneys, as do at least the primitive members of most other molluscan classes. These organs are rarely strictly bilaterally symmetrical, and then probably secondarily, because of the differential growth accompanying the helical coiling of the body. Their internal anatomy also shows features which are often regarded as primitive – the rectum penetrates the ventricle, nerve cells are common in nerves as well as in ganglia, the male lacks a copulatory organ and, usually, glands on the female duct are absent. Gametes are broadcast and fertilisation is external, a reproductive mode compatible only with the marine habitat. The larvae are trochophores, similar to those of annelids and platyhelminths, with which molluscs also share the spiral pattern of cleavage; free larval life is usually brief. Other characters found in most vetigastropods are probably not primitive, although they have been regarded as such. They include the polydont radula (many teeth in each transverse row), a spiral caecum at the posterior end of the stomach and many external sensory tentacles and papillae.

Ancestral gastropods were marine, but which particular marine habitat they occupied is uncertain. Hard-bottomed, shallow sublittoral habitats may have been favoured, particularly in view of the putative ancestral methods of locomotion and feeding. They were probably detrital feeders, ingesting predominantly vegetable matter, perhaps with some incidental admixture of animal substance, either in the form of small, sessile or sedentary animals or as broken fragments. From some such beginnings, the gastropods underwent several extensive radiations, some of them spectacular among animal groups (Purchon 1968; Graham 1985; Erwin & Signor 1991; Ponder & Lindberg 1997).

Although most of the 'prosobranchs' are marine, some live in freshwater and a few groups have become terrestrial, particularly in humid tropical areas. Migration to freshwater and land probably occurred via estuarine habitats, although a few groups appear to have become terrestrial by adaptation to higher and higher levels on the seashore. Among the latter are the Northern Hemisphere littorinoidean families Pomatiastidae and Chondropomidae, and the cosmopolitan Assimineidae and Truncatellidae (both Rissooidea). In the Rissooidea alone, five families have independently invaded freshwater, and three have some terrestrial members (Ponder 1988a).

The problems overcome by these animals are the same as those confronting all animals that have entered freshwater and terrestrial environments, and affect their respiration, water relations, and reproductive habits in particular (see also Chapter 1). Acquisition of internal fertilisation was one of the main prerequisites, and was achieved in the older 'prosobranch' non-marine groups, all Palaeozoic in origin, including the Cyclophoroidea (exclusively terrestrial), Ampullarioidea (exclusively freshwater) and Neritopsina (marine, freshwater and terrestrial). Two of these groups appear to be the most primitive amongst extant members of their primarily marine clades – the Helicinidae in Neritopsina (Bourne 1911; Baker 1925; Hedegaard 1990) and Cyclophoroidea in Caenogastropoda (Ponder & Lindberg 1997). The non-architaenioglossan terrestrial Caenogastropoda (some Littorinoidea and Rissooidea) are relatively recent in origin, whereas two older (Mesozoic) caenogastropod groups produced significant multiple freshwater radiations (Cerithioidea, Houbriek 1988; Rissooidea, Ponder 1988a).

Some gastropods have adopted a planktonic or nectonic life. Species of *Janthina* use a raft of bubbles trapped in mucus, but the predatory heteropods (Caenogastropoda) and Gymnosomata (Opisthobranchia) are active swimmers. Some other gastropods which are normally benthic (a few vetigastropods and neogastropods, as well as some opisthobranchs) swim less actively, using undulating movements of the foot.

PHYLOGENY AND CLASSIFICATION

There was a great deal of interest in the higher classification of gastropods in the 19th Century (see Ponder & Warén 1988 and Bieler 1992a for references to early summaries), with many schemes proposed that were usually founded primarily on one or two organ systems [for example, radulae, Troschel (& Thiele) 1856–1893; nervous system, Bouvier 1887]. The publication of the gastropod part of Thiele's (1929–1935) *Handbuch*, in which the familiar gastropod classification was elaborated from that proposed earlier by Thiele (1925a), effectively stifled interest in the higher classification of gastropods until the 1980s. Thiele modified Milne-Edwards' (1848) concept of three subclasses, Prosobranchia, Opisthobranchia and Pulmonata (see Fig. 15.1A), and this arrangement was used almost universally until recently. Thiele also divided the Prosobranchia into the primitive Archaeogastropoda, the middle Mesogastropoda and the advanced Stenoglossa (= Neogastropoda; Wenz 1938–1944). These three groupings implied progressively 'improved' levels of organisation and this simplistic way of viewing gastropod evolution became firmly entrenched. Thiele's classification was used in the synoptic works of Wenz (1938–1944), Cox (1960b) and Boss (1982). Cox (1960a) proposed Caenogastropoda for mesogastropods and neogastropods, but otherwise there were few modifications. As noted above, it is now generally agreed that the Prosobranchia is paraphyletic and that subdivision into the Archaeogastropoda, Mesogastropoda and Neogastropoda simply recognises grades of organisation. In the last few decades, the classification and phylogeny of 'prosobranchs' has slowly been modified as seen in the following publications: Kosuge (1966a), Ponder (1973a), Golikov & Starobogatov (1975), Salvini-Plawen (1980), Fretter & Graham (1982), Haszprunar (1985a, 1985b, 1988a, 1988b, 1993), Lindberg (1986a, 1988a), Hickman (1988), Ponder & Warén (1988), Bieler (1992a) and Ponder & Lindberg (1996, 1997). Some of these changes are discussed briefly below.

Since the 1980s there has been an upsurge in interest in the phylogeny of gastropods (Salvini-Plawen 1980, 1990; Graham 1985; Haszprunar 1985a, 1985b, 1985d, 1988a, 1988b; Salvini-Plawen & Haszprunar 1987; Bieler 1992a; Ponder & Lindberg 1996, 1997) and this continues today. In particular, the major analysis of 'prosobranch' phylogeny of Haszprunar (1988a) (Fig. 15.1C) has been a watershed on the subject, although criticised for its methodology (Bieler 1990; Haszprunar 1990). Four major hypotheses of gastropod phylogeny are summarised in Figure 15.1. A computer-based cladistic analysis of gastropod phylogeny was recently undertaken by Ponder & Lindberg (1996); see Figure 15.1D. A gastropod phylogeny further developed by Ponder & Lindberg (1997) is shown in Figure 15.2. For the greater part the gastropod classification used here follows Ponder & Lindberg (1997) as set out in Table 15.1 and depicted in Figure 15.2. The characters and character states upon which the phylogeny and thus classification are based, and arguments for assigned polarities, are discussed in detail by Ponder & Lindberg (1996, 1997).

The position of the Neritoidea, included in the Archaeogastropoda by Thiele has been the subject of some debate (Yonge 1947). The group was excluded from the Archaeogastropoda by J.E. Morton & Yonge (1964), although this was not generally followed. Kosuge (1966a) proposed the Heterogastropoda for triphorids and several groups now included in the Heterobranchia (for example, Architectonicidae). Golikov & Starobogatov (1975) divided the 'prosobranchs' into three subclasses (Fig. 15.1B), retained the Pulmonata and Opisthobranchia, and with little justification created a large number of other high rank taxa. Minichev & Starobogatov (1979) modified this scheme and also added substantially to the number of available higher taxa.

As already attested, a number of taxa previously included in the 'prosobranchs' are actually heterobranchs. Fretter & Graham (1949) and Fretter (1953) showed that the Pyramidellidae are anatomically closer to opisthobranchs than to 'prosobranchs' because they have such features as a heterostrophic protoconch, ciliated ridges in the mantle cavity, no ctenidium, folds on the columella of the shell and chalazae between the eggs. These links were not so obvious in the anatomical studies of Fretter (1948) on another two groups of heterobranchs, the minute Rissoellidae and Omalogyridae, and these groups continued to be regarded as 'prosobranchs' until recently when the heterobranch relationship of all these families, suspected by Fretter & Graham (1962), was confirmed, along with that of the larger Architectonicidae and Mathildidae, by investigation of their sperm structure (Healy 1982a, 1988a, 1988b, 1993), osphradial structure and general anatomy (Haszprunar 1985b, 1985d, 1985e, 1985f). Haszprunar's (1985b) concept of the Heterobranchia included the opisthobranchs and pulmonates (= Euthyneura), as well as the streptoneuran opisthobranch-like 'prosobranchs'. He called this latter group Allogastropoda (Haszprunar 1985b) or Triganglionata (Haszprunar 1985d), and argued that they are the most primitive heterobranchs. This group is also referred to as Heterostrophia by Golikov & Starobogatov (1975) and Ponder & Warén (1988). Members of another group long included among the 'prosobranchs', the Valvatoidea, were also shown to be heterobranchs (Haszprunar 1988a; Rath 1988; Ponder 1991a). These groups of lower heterobranchs are included at the end of this chapter because they have been historically regarded as prosobranchs.

The archaeogastropods were assigned to three suborders by Salvini-Plawen (1980): the Vetigastropoda (a new name for most of the traditional archaeogastropods), the Docoglossa and the Neritopsina. Graham (1985) reviewed gastropod classification and agreed with Golikov & Starobogatov (1975) that the docoglossan limpets (now Patellogastropoda, Lindberg 1986a, 1988a) are very different from other gastropods.

Archaeogastropoda is a grade (Haszprunar 1988a, 1988b; Hickman 1988), although a major part of this grouping, the Vetigastropoda (Salvini-Plawen 1980) is probably monophyletic (Salvini-Plawen 1980; Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a). Thiele's concept of the Mesogastropoda is

Table 15.1 A summary of the major gastropod groups recorded from the Australian region. Families not yet recorded from Australia, but likely to occur here, are indicated with an asterisk. The families are ordered in the sequence followed in the text. (See Introduction, section on Phylogeny and Classification, and Figures 15.1 and 15.2 for explanation.) † Neotaenioglossa is a paraphyletic group comprising Cerithioidea through to Carinarioidae. †† See Chapter 16. ††† See Chapter 17. ‡ Family introduced into Australia, see pp. 71 and 706. § See superfamily Pryamidelloidea p. 865.

Subclass EOGASTROPODA

Order PATELOGASTROPODA

Suborder PATELLINA

- Superfamily PATELLOIDEA
- Family Patellidae

Suborder NACELLINA

- Superfamily NACELLOIDEA
- Family Nacellidae
- Superfamily ACMAEOIDEA
- Family Acmaeidae
- Family Lepetidae
- Family Lottiidae

Subclass ORTHOGASTROPODA

Superorder COCCULINIFORMIA

- Superfamily COCCULINOIDEA
- Family Cocculinidae
- Family Bathysciadiidae
- Superfamily LEPETELLOIDEA
- Family Lepetellidae*
- Family Pseudococculinidae
- Family Osteopeltidae*
- Family Cocculinellidae
- Family Choristellidae

Superorder VETIGASTROPODA

- Superfamily PLEUROTOMARIOIDEA
- Family Pleurotomariidae
- Family Scissurellidae
- Family Haliotidae
- Superfamily FISSURELLOIDEA
- Family Fissurellidae
- Superfamily TROCHOIDEA
- Family Turbinidae
- Family Trochidae
- Family Skeneidae
- Family Pendromidae
- Superfamily SEGUENZIOIDEA
- Family Seguenziidae

Superorder NERITOPSINA

- Superfamily NERITOIDEA
- Family Neritopsidae
- Family Neritidae
- Family Phenacolepadidae
- Family Titiscaniidae
- Family Hydrocenidae
- Family Helicinidae

Superorder CAENOGASTROPODA

Order ARCHITAENIOGLOSSA

- Superfamily CYCLOPHOROIDEA
- Family Cyclophoridae
- Family Pupinidae
- Family Diplommatinidae
- Superfamily AMPULLARIOIDEA
- Family Viviparidae
- Family Ampullariidae‡

Order SORBEOCONCHA (Neotaenioglossa†)

Superfamily CERITHIOIDEA

- Family Cerithiidae
- Family Dialidae
- Family Litiopidae
- Family Turritellidae
- Family Siliquariidae
- Family Batillariidae
- Family Planaxidae
- Family Potamididae
- Family Thiaridae
- Family Diastomatidae
- Family Modulidae
- Family Scaliolidae

Superfamily CAMPANILOIDEA

- Family Campanilidae
- Family Plesiotrochidae

Suborder HYPGASTROPODA

Infraorder LITTORINIMORPHA

Superfamily LITTORINOIDEA

- Family Littorinidae
- Family Pickworthiidae

Superfamily CINGULOPSOIDEA

- Family Cingulopsidae
- Family Eatoniellidae
- Family Rastodentidae

Superfamily RISSOOIDEA

- Family Barleeidae
- Family Anabathridae
- Family Emblandidae
- Family Rissoidae
- Family Epigridae
- Family Iravadiidae
- Family Hydrobiidae
- Family Pomatiopsidae
- Family Assimineidae
- Family Truncatellidae
- Family Elachisinidae
- Family Bithyniidae
- Family Caecidae
- Family Hydrococcidae
- Family Vitrinellidae
- Family Stenothyridae

Superfamily STROMBOIDEA

- Family Strombidae
- Family Struthiolariidae

Superfamily VANIKOROIDEA

- Family Hipponicidae
- Family Vanikoridae
- Family Haloceratidae

Superfamily CALYPTRAEOIDEA

- Family Calyptraeidae

Superfamily CAPULOIDEA

- Family Capulidae

Superfamily XENOPHOROIDEA

- Family Xenophoridae

Superfamily VERMETOIDEA

- Family Vermetidae

Superfamily CYPRAEOIDEA

- Family Cypraeidae
- Family Ovulidae

Superfamily VELUTINOIDEA

- Family Triviidae
- Family Velutinidae

Superfamily NATICOIDEA

- Family Naticidae

Superfamily TONNOIDEA

- Family Bursidae
- Family Cassidae
- Family Ficidae
- Family Laubieridae
- Family Personidae
- Family Pisanianuridae
- Family Ranellidae
- Family Tonnidae

Superfamily CARINARIOIDEA

- Family Atlantidae
- Family Carinariidae
- Family Pterotracheidae

Infraorder PTENOGLOSSA

Superfamily TRIPHOROIDEA

- Family Triphoridae
- Family Cerithiopsidae

Superfamily JANTHINOIDEA

- Family Janthinidae
- Family Epitoniidae
- Family Aclididae

Superfamily EULIMOIDEA

- Family Eulimidae

Infraorder NEOGASTROPODA

Superfamily MURICOIDEA

- Family Muricidae
- Family Turbinellidae
- Family Buccinidae
- Family Columbelloidae
- Family Nassariidae
- Family Melongenidae
- Family Fasciolaridae
- Family Volutidae
- Family Olividae
- Family Harpidae
- Family Marginellidae
- Family Mitridae
- Family Volutomitridae
- Family Costellariidae

Superfamily CANCELLARIOIDEA

- Family Cancellariidae

Superfamily CONOIDEA

- Family Turridae
- Family Terebridae
- Family Conidae

Superorder HETEROBRANCHIA

Superfamily VALVATOIDEA

- Family Cornirostridae
- Family Orbitestellidae
- Family Xylodisculidae

Superfamily ARCHITECTONICOIDEA

- Family Mathildidae
- Family Architectonicidae

Superfamily RISSOELLOIDEA

- Family Rissoellidae

Superfamily OMALOGYROIDEA

- Family Omalogyridae

Superfamily PYRAMIDELLOIDEA

- Family Pyramidellidae
- Family Amathinidae
- Family Cimidae§
- Family Donaldinidae§
- Family Ebalidae§

Order OPISTHOBRANCHIA††

Order PULMONATA†††

15. PROSOBRANCHS

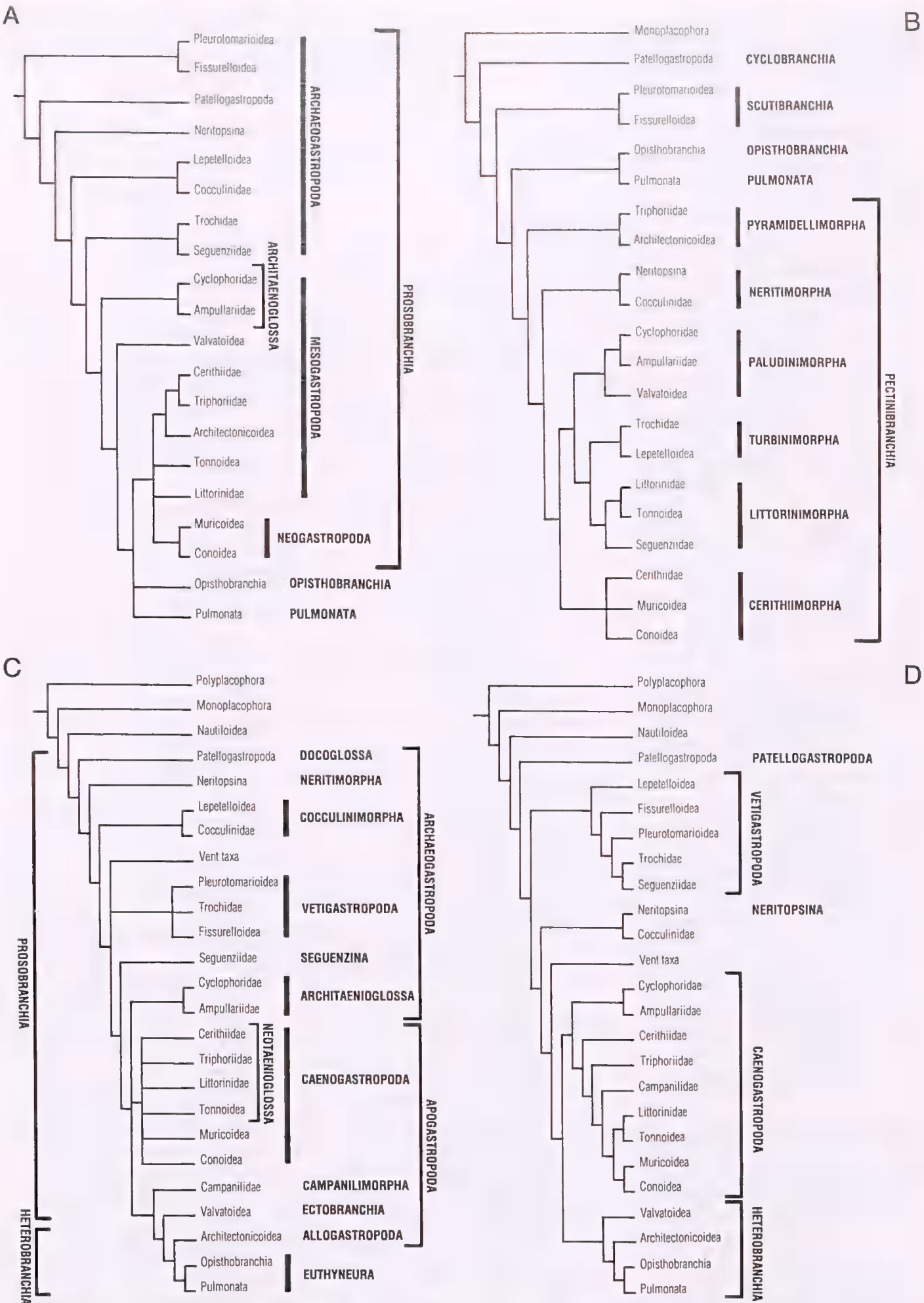


Figure 15.1 Four major phylogenetic schemes proposed for the Gastropoda. The family-level taxa represented in the analysis are only a representative subset of each major group. A, Thiele [1929–(1935)]; B, Golikov & Starobogatov (1975); C, Haszprunar (1988a); D, Ponder & Lindberg (1996). (Modified after Ponder & Lindberg 1996)

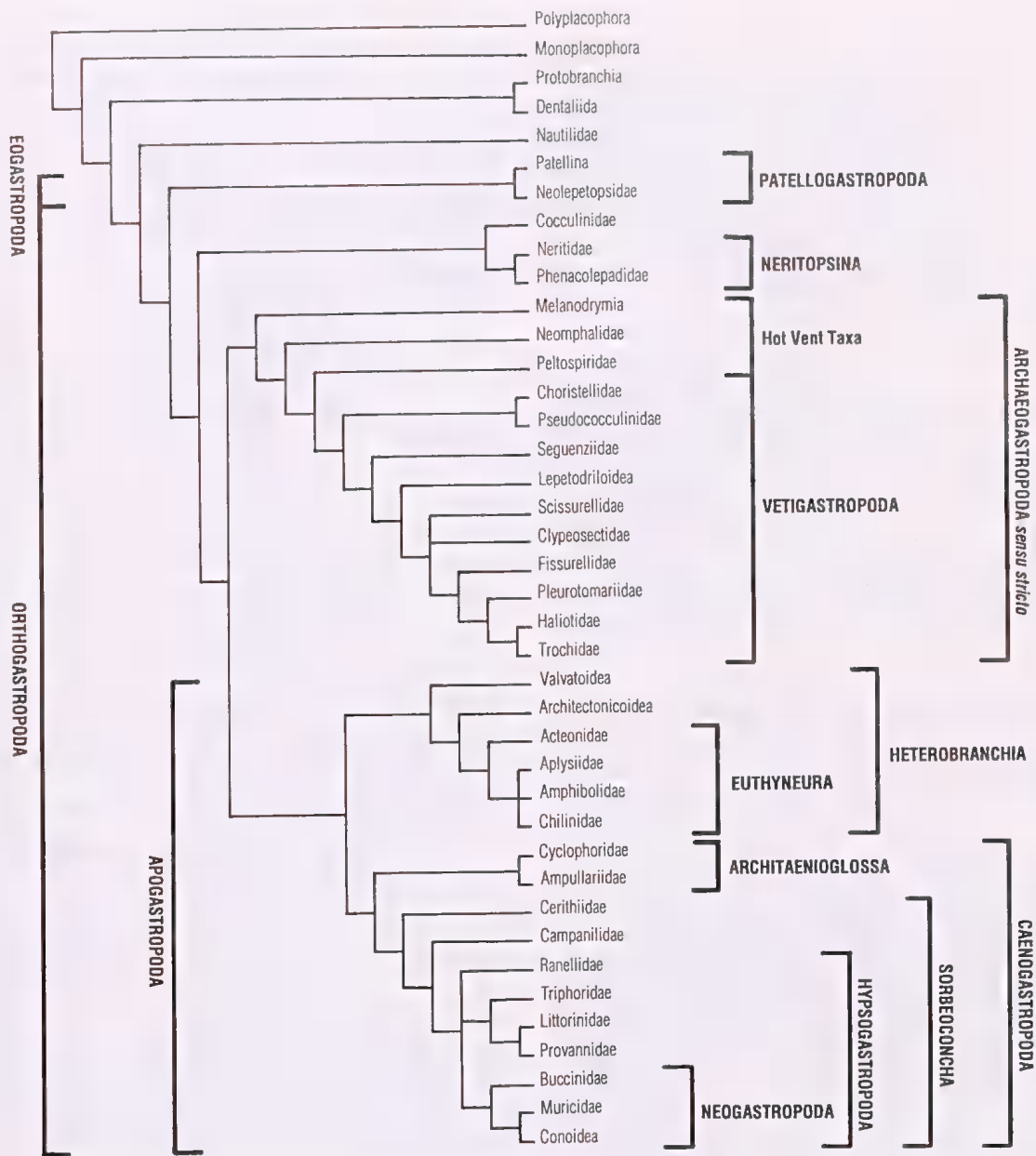


Figure 15.2 Ponder and Lindberg's more recent scheme for the phylogeny of the Gastropoda. The family-level taxa indicated in the analysis are only a representative subset of each major group. (After Ponder & Lindberg 1997) [I. Hallam]

also seen as a grade (Graham 1985; Haszprunar 1988a). However, among several recently discovered new gastropod groups from hydrothermal vents (Fretter, Graham & McLean 1981; Fretter 1988, 1989, 1990; McLean 1988a, 1988b, 1989a, 1989b; Haszprunar 1989a; Warén & Bouchet 1989, 1993; Warén & Ponder 1991; Beck 1992a, 1992b, 1993) are some which share features that seem to link caenogastropods and vetigastropods. This may not signify a close relationship as they are mainly shared primitive features or parallel developments in some features such as loss of the right pallial complex.

It is now clear that the Patellogastropoda is the sister group to all other gastropods. This group, together with its extinct coiled ancestors, was named Eogastropoda by Ponder & Lindberg (1996). The Orthogastropoda comprises all the remaining 'prosobranchs' (see Fig. 15.2) – vetigastropods, neritopsines, cocculiniform groups, hot-vent groups (an unnamed clade), caenogastropods (Mesogastropoda + Neogastropoda) and also the heterobranchs (including opisthobranchs + pulmonates). Some support for the scheme now recognised has been obtained from molecular data (Tillier, Masselot, Hervé & Tillier 1992; Tillier, Masselot, Guerdoux & Tillier 1994), although other work (Rosenberg, Kuncio, Davis & Harasewych 1994) appears to contain some discrepancies. These studies are still in their infancy but are essential for testing of recent phylogenetic hypotheses.

The major gastropods groups are summarised briefly below. Additional information can be found under the headings for individual groups in this chapter. Note that the ranks assigned to each group are purely arbitrary. Authors of some classifications may choose to use higher ranks (for example, the superorders might be subclasses). Differences in rank are unimportant – what matters is the relationship of the taxa, that is their relative positions on a phylogenetic tree.

Subclass Eogastropoda

The only extant eogastropods are the 'true limpets', the Patellogastropoda. These are described in detail elsewhere in this chapter. In addition to their 'docoglossan' stereoglossate radula, patellogastropods have many distinctive shell structural and anatomical characters (see Lindberg 1988a; and herein).

Subclass Orthogastropoda

All the remaining gastropods belong to the Orthogastropoda and are distinguished by a number of anatomical characters, including having a flexiglossate radula. The major groups of non-heterobranch orthogastropods are outlined briefly below.

15. PROSOBRANCHS

Superorder Cocculiniformia

Haszprunar (1988c) proposed the Cocculiniformia to encompass what he considered a monophyletic group. However, Ponder & Lindberg's (1996, 1997) analyses indicate that it is polyphyletic, composed of two very different groups of limpets. The Lepetelloidea may be modified vetigastropods whereas the Cocculinoidea are of uncertain affinities, possibly a sister group to neritopsines. With only two exceptions (for example, the coiled genus *Choristella*), all members of the cocculiniform group are small limpets, mostly from deep water, and live on biogenic substrata such as bone and wood.

Superorder Vetigastropoda

This group includes the Pleurotomarioidea (often divided into Haliotoidea, Scissurelloidea and Pleurotomarioidea), Fissurelloidea and Trochoidea. These superfamilies all share a mixture of primitive and advanced features. Amongst the primitive features are the bipectinate ctenidia with gill membranes (although the filaments contain skeletal rods, as in caenogastropods), and the general features of the alimentary canal and nervous system. Advanced features found only in members of this group (synapomorphies) include bursicles, sensory papillae, epipodial sense organs, a modified left kidney (papillary sac), an outer egg-envelope, a spiral gastric caecum and the papillate oesophageal gland.

The Seguenzoidea appears to have its closest affinities with Trochoidea and is here included in the Vetigastropoda.

Superorder Neritopsina

This ancient (Devonian to Recent) group includes the Neritoidea (extant families: Neritopsidae, Neritidae, Phenacolepadidae, Titiscaniidae, Hydrocenidae and Helicinidae) (Cox 1960b). A number of anatomical characters set Neritopsina apart from other orthogastropods. They share a number of primitive features (for example, the rhipidoglossate radula) with vetigastropods, and the lack of ctenidial skeletal rods with patellogastropods, but resemble caenogastropods in having glandular pallial genital ducts and planktotrophic larvae. Neritopsines occur in marine, terrestrial and freshwater habitats, and have body forms ranging from snail-like to limpet-like to slug-like.

Superorder Caenogastropoda

Caenogastropods appear later in the fossil record than members of other groups, the first record being in the Ordovician (Bandel 1993a). The first undoubted neogastropods do not appear until the Cretaceous (Taylor, J.D. & Morris 1988). The terrestrial Cyclophoroidea and the freshwater Ampullarioidea which make up the Architaenioglossa are the most primitive living caenogastropods and may or may not be monophyletic.

The caenogastropod radula has undergone oligomerisation. Most caenogastropods have only one pair of lateral teeth, and two pairs of marginal teeth. The salivary glands no longer overlie the buccal-wall as they do in vetigastropods but have migrated posteriorly and connect with the buccal cavity by means of long ducts. The intestine is shortened markedly and straightened and does not penetrate the ventricle. The vascular system has lost the right pallial component and the left kidney carries out the excretory activity of the right kidney of vetigastropods and patellogastropods, in addition to the role of the original left kidney of regulating the solute content of the blood and resorbing organic solutes (Delhaye 1976; Andrews, E.B. 1985).

The nervous system is noticeably more compact than in patellogastropods and vetigastropods. In the Sorbeoconcha (all Caenogastropoda excluding Architaenioglossa), the pedal cords have shortened to ovoid ganglia in nearly all groups and all have an epiathroid nervous system in which pleural ganglia lie close to cerebral ganglia. The cerebral ganglia in turn have migrated backwards so that they lie behind the buccal mass over the pedal ganglia, and the six ganglia form a ring round the oesophagus.

As in neritopsines and heterobranchs the reproductive system is modified for internal fertilisation with the development in many groups of copulatory organs, or other means of internal fertilisation, and the ability to protect and provide food for embryos. Consequently, caenogastropod embryos can develop further before hatching than patellogastropod and vetigastropod embryos and have developed larval planktotrophy. Some taxa may eliminate all larval stages, a prerequisite for invasion of non-marine habitats by a number of different caenogastropod groups.

The Caenogastropoda was divided by Thiele (1929–1935) into two main groups: the Mesogastropoda and the Neogastropoda. The majority of Thiele's mesogastropods were referred to the Neotaenioglossa by Haszprunar (1985a) and Ponder & Warén (1988). The most primitive of the extant neotaenioglossan superfamilies is probably the Cerithioidea which shares some unique sperm ultrastructural characters with architaenioglossans (Healy 1988a). Neogastropods probably share an ancestor with one of the other neotaenioglossan groups as they too share some distinctive sperm (and other) characters (Healy 1988a; Ponder & Lindberg 1997). Consequently, it is now clear that Thiele's Mesogastropoda and Haszprunar's Neotaenioglossa are both paraphyletic. Ponder & Lindberg (1997) recognised two major monophyletic groups at different levels among Caenogastropoda: the Sorbeoconcha and the Hypsgastropoda. Hypsgastropoda, referred to as the 'higher caenogastropods', is a subset of Sorbeoconcha and comprises all sorbeoconchs (including neogastropods) minus cerithioideans and campaniloideans (see Fig. 15.2).

Within the 'neotaenioglossan' Hypsgastropoda are a number of very distinct groups. Typically, as the name suggests, they have a taenioglossate radula, as well as acinous salivary glands, a glandular oesophagus, a hypobranchial secretion which is not purple, the pallial oviduct is closed and a penis is present in males. Contrasted with these is the rather heterogeneous assemblage referred to the Ptenoglossa [= Ctenoglossa and Heteroglossa (Haszprunar 1985a) in part the Heterogastropoda of Kosuge (1966a)]. In many members of the Ptenoglossa, the radula is not taenioglossate, having many more than seven teeth per row, and these often all similar. The species in this group are all carnivorous on particular groups of invertebrates: the Triphoroidea specialising on sponges, the Janthinoidea on cnidarians and the Eulimoidea on echinoderms. Triphoroideans and janthinoideans share a set of anatomical features that sets them apart, including an oesophagus either devoid of special glands or with glands with anomalous relationships, an open female pallial duct, and no penis in males. Janthinoideans have purple hypobranchial secretions and tubular salivary glands. Some authors have, probably wrongly, suspected a relationship between members of this group and taxa now regarded as primitive heterobranchs (for example, Robertson 1963a, 1973a; Andrews, E.B. 1991). The neotaenioglossan and ptenoglossan assemblages among caenogastropods are not well formulated and both require urgent attention in future phylogenetic studies.

There are several significant differences between neotaenioglossans and neogastropods, mainly in the anterior gut (Ponder 1973a), as neogastropods are almost exclusively carnivorous. Neogastropods (and some neotaenioglossans) have a proboscis which is retractile within a sheath. However, neogastropods differ from the carnivorous neotaenioglossan groups in that the number of radula teeth is reduced from seven to five or fewer per transverse row in toxoglossans (Conoidea) or three or less in rachiglossans (or stenoglossans) (Muricoidea). Correlated with the formation of the proboscis, a valve (valve of Leiblein) has developed in the oesophageal region of muricoideans which prevents regurgitation when the proboscis is extended. In addition, the oesophageal gland has split from the main channel of the oesophagus in all neogastropods to form a glandular mass (gland of Leiblein in Muricoidea, poison gland in Conoidea) linked to it only by a narrow duct. Correlated with the carnivorous diet, the stomach is secondarily simplified in all neogastropods.

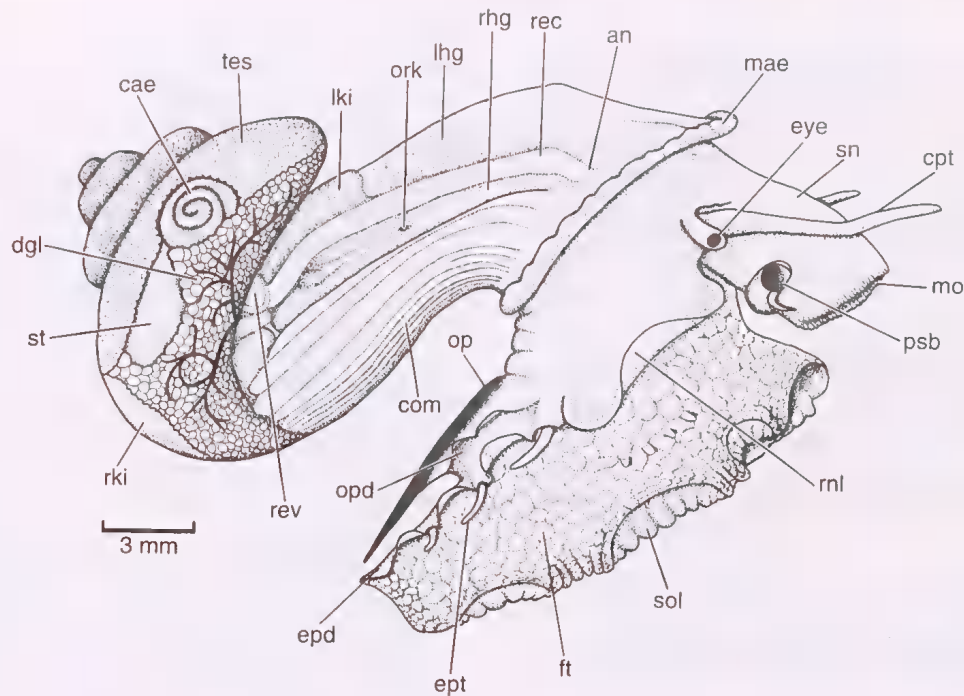


Figure 15.3 *Calliostoma zizyphinum* (Vetigastropoda, Trochidae), male removed from shell, viewed from the right; some organs are seen by transparency. an, location of anus; cae, spiral caecum of stomach; com, columellar muscle; cpt, cephalic tentacle; dgl, digestive gland; epd, epipodium; ept, epipodial tentacle; eye, eye; ft, foot; lhg, left hypobranchial gland; lki, left kidney (papillary sac); mae, mantle edge; mo, mouth; op, operculum; opd, opercular disk; ork, opening of right kidney (urinogenital opening) inside mantle cavity; psb, pseudoproboscis; rec, rectum; rev, rectum within ventricle; rhg, reduced right hypobranchial gland; rki, right kidney; rnl, right neck lobe; sn, snout; sol, sole of foot; st, stomach; tes, testis. (After Fretter & Graham 1962) [B. Scott]

MORPHOLOGY AND FUNCTION

The Shell, Foot, Muscular System and Locomotion

When a snail such as a *Calliostoma* species emerges from its shell, the foot and operculum are protruded along with the head. The head bears a large snout, a pair of long, tapering, cephalic tentacles and narrow eye stalks (Figs 15.3, 15.6). The protrusion of the animal results from the action of part of the columellar muscle pushing the snail out of the shell. On withdrawal another part of the columellar muscle contracts. The foot is broad anteriorly, and immediately behind its anterior margin a deep transverse groove marks the opening of the anterior pedal gland, which produces most of the mucus over which the snail creeps. This anterior groove separates the dorsal propodium from the broad mesopodium or creeping sole of the foot. An epipodium, a projecting upper border of the foot, with epipodial tentacles is present in *Calliostoma* (Fig. 15.3); as well as in many other vetigastropods. The operculum is attached to the skin of the opercular (or operculigerous) lobe or disk which lies dorsally on the foot (Fig. 15.3).

The sole of the foot contains a complex array of muscles, some aligned dorso-ventrally, others transversely or longitudinally through haemocoelic spaces (Voltzow 1988, 1994). The mechanism of locomotion has been described by Vlès (1907), Parker (1911), Lissmann (1945, 1946), Jones & Trueman (1970) and S.L. Miller (1974b), but these earlier works missed the importance of mucus in locomotion as well as adhesion. Denny (1984) has shown how the physical properties of pedal mucus limit the size and speeds of gastropods. S.L. Miller (1974b) also discussed pedal activity in relation to habitat and mode of life.

Creeping is achieved through the passage of a series of waves of local contraction and relaxation of the pedal musculature over the mesopodial sole. These may be direct, starting posteriorly, or retrograde, starting anteriorly, and either monotaxic, covering the whole breadth of the sole, or ditaxic, two series out of phase with one another and each occupying half the breadth of the sole. In direct waves (Fig. 15.4D–F) forward movement results from

shortening of the leading half of the advancing wave; in retrograde waves (Fig. 15.4A–C) it results primarily from elongation in the leading half of the backwardly moving wave. In streptoneuran gastropods, movement occurs more frequently by means of ditaxic and retrograde waves than by monotaxic or direct waves, although there is little connection between wave form and direction and taxonomic position. Direct waves are known to occur in some haliotids, trochids, pomatiasids, truncatellids, calyptraeids, naticids and muricids, as well as in pulmonates (see Fig. 14.9A). The wavelength of a direct wave is commonly less than that of a retrograde one, and that of a ditaxic wave a little less than that of a monotaxic one. Both occasionally equal the total length of the foot, as occurs in some turbinids and the European genus *Pomatias* (Fig. 14.9B), the animal moving the whole length of each side of the foot alternately, in a single step.

The locomotor waves are generated by the local contraction of the dorso-ventral muscles which lift the sole off the substratum. The increased length of the raised surface stretches the epithelium and distorts the vesicles above it. Contraction of the dorso-ventral muscles produces a negative pressure of as much as 150 mm of water beneath each wave and a suction on the water and mucus beneath the foot. As the muscles contract at the leading edge of the wave and create a negative pressure they antagonise the muscles at the lagging edge so that these relax and the sole restores its contact with the substratum. Progression of the pedal waves is thus brought about by the antagonistic action of muscles and involves an internal hydrostatic skeleton and an external hydraulic system (Fretter & Graham 1994; Voltzow 1994).

Three important features of the foot concerned with locomotion are: the elasticity of the epithelium of the sole; the numerous vesicles above the epithelium, which are haemocoelic according to Jones & Trueman (1970) and termed 'space cells' by Grenon & Walker (1982); and the extrinsic and intrinsic muscles. The extrinsic muscles are dorso-ventral fibres of the columellar muscle which pass between the vesicles to insert on the epithelium. Dorsal to these are the transverse strands of the intrinsic muscles, which prevent increase in the breadth of the sole on contraction. Apparently, no longitudinal muscles are involved though some run between the transverse fibres.

15. PROSOBRANCHS

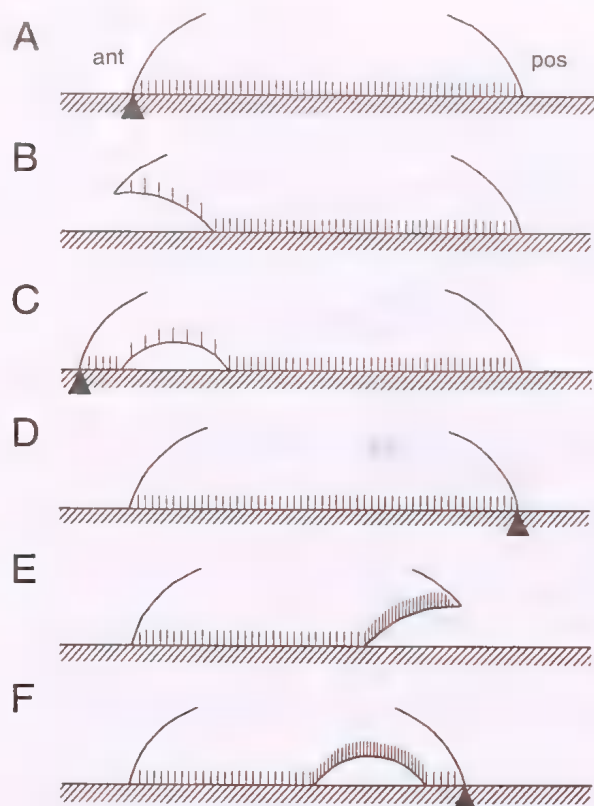


Figure 15.4 Diagrams showing the initiation and propagation of locomotor waves along the sole of the foot of a gastropod. The direction of movement of the snail is in every case from right to left (ant, anterior; pos, posterior). Short vertical lines mark equal distances along the resting foot (A, D). These move apart where elongation occurs and become closer where the sole is contracted. The arrow heads indicate the distance moved; compare A–C and D–F. A–C, retrograde wave: A, foot at rest in contact with the substratum; B, anterior tip raised by contraction of dorso-ventral muscles (not shown) and extended forward; C, anterior tip re-attached and wave of leading edge elongation starting to move backwards. D–F, direct wave: D, foot at rest in contact with the substratum; E, posterior tip raised by contraction of dorso-ventral muscles and shortened; F, posterior tip re-attached and wave of leading edge shortening, starting to move forwards. (Modified from Fretter & Graham 1994) [B. Scott]

S.L. Miller (1974b) argued that retrograde waves are the more primitive of the two wave types, partly because of their more frequent occurrence in lower gastropods and because they are also found in chitons. Similarly monotaxic waves are taken to be more primitive than ditaxic. The advantages of ditaxic waves were discussed by Lissmann (1945), J.E. Morton (1979) and S.L. Miller (1974b); they enable animals to turn in a restricted area by altering the rate of wave travel on one side of the foot relative to that on the other (see also reviews in Fretter & Graham 1994 and Voltzow 1994).

Other types of waves have been described, as well as locomotor methods which seem to dispense altogether with any regularity in wave production. Diagonal waves, which are always ditaxic but may be either direct or retrograde, start in the midline of the foot posteriorly or anteriorly and move to the antero-lateral or postero-lateral corners, right and left sets alternating and diverging. Although the direction of wave movement is oblique each point on the wave front is moved directly anteriorly (for example, in some cypraeids and neogastropods such as some muricids, buccinids and columbellids). Several unique wave-based patterns, termed composite waves by Olmsted (1917), are seen in Cypraeidae. In many species of *Cypraea* (Miller, S.L. 1974b), a series of waves crosses the foot from side to side, although the direction of movement of points on the sole is anterior. As these are compression waves they have presumably been derived from an ancestral direct wave pattern. A set of waves may cross the sole in one direction in the anterior half and in the opposite direction posteriorly, an arrangement which allows rapid change in direction, though demanding an unexpectedly high degree of nervous control.

In some caenogastropods, movement seems to result from the formation of irregular areas, perhaps representing a degenerate form of retrograde wave movement since these areas elongate. This mechanism occurs widely among neotaenioglossans and neogastropods, but it seems to be particularly common in those with tall shells (for example, cerithiids, terebrids), those which are relatively immobile (some of which may also have tall shells, such as turritellids and epitioids), and in such families as the Cymatiidae and at least some Capulidae. Cilia alone provide an efficient means of movement for many small gastropods, and even for some of considerable size such as species of *Cassis*, *Nassarius* and *Polinices*. Since it gives rise to a gliding motion over the substratum and does not involve the degree of adhesion necessary for wave movement, ciliary action is appropriate for travel over loose or unstable substrata, and is facilitated by a foot of large area. On soft substrata, and even in some other circumstances, ciliary movement is faster than locomotor waves, but has the disadvantage of being unidirectional.

Leaping, or at least lurching, has evolved in more than one group, sometimes as the habitual method of locomotion, sometimes as part of an escape reaction. Stepping occurs in groups such as Stromboidea (Weber 1925; Berg 1974; J.E. Morton 1951a) and in another related superfamily, Xenophoroidea (Linsley & Yochelson 1973), and may have led to the leaping or lurching mode. In *Aporrhais* and strombids, the foot is released from the substratum and extended forward and re-attached, followed by a contraction of the columellar muscle which pulls the shell forward in one step (see Fig. 14.10). An analogous device has also evolved in some nassariid whelks which use it in an escape tactic if attacked by starfish (Weber 1924). When touched by tube-feet the whelk contracts the columellar muscle in such a way that the visceral mass and shell are twisted on the head-foot until the mantle cavity faces backwards; the head-foot then follows it into this orientation and the snail creeps off in a new direction. Speed of escape from predators may be increased by lengthening each locomotor wave, which effectively lengthens the 'stride', as in the American trochid genus *Tegula* (Miller, S.L. 1974a), or by increasing the speed of travel of the wave, as in *Calliostoma* species (Miller, S.L. 1974b), or perhaps by both. Denny (1984) has shown that escape responses ('running') in *Haliotis* species are achieved by lifting the foot and allowing the seawater to reduce the viscosity of the mucous layer between the foot and the substratum.

As part of its locomotive role, the foot is glandular, secreting material to lubricate the surface over which the sole travels and to aid adhesion (tenacity). The lubricant comes partly from the anterior pedal gland opening to the groove between propodium and mesopodium, and partly from the sole gland (epithelial goblet cells and subepithelial gland cells). The secretion, from several types of cell, is a mixture of substances, such as mucopolysaccharide and mucoprotein, and has been most fully analysed in two European patellogastropod limpets by Grenon & Walker (1978). Lindberg & Dwyer (1983) found similar gland systems in the North American patellogastropod '*Collisella*' *scabra*.

The specialised posterior pedal gland, presumably arising as a hypertrophied area of the sole gland and opening in the posterior half of the sole, is commonly found in many small caenogastropods. Its secretion forms a rope of mucus which is grasped by the rear part of the foot. It may be attached to various structures in the snail's environment, like a spider's thread, and the snail may climb along it free from the substratum to which it must otherwise cling.

The tenacity with which a gastropod adheres to the substratum reaches a maximum in patellogastropods. Although not fully understood, it is probably partly due to contraction of dorso-ventral pedal muscles raising the sole from the substratum to produce a negative pressure (suction), the contact between the margin of the foot and the substratum being sealed by pedal secretions. This suction does not, however, fully account for the total adhesion as limpets can withstand forces much greater (up to 35 g.mm⁻²; Fischer 1948) than possible from suction alone.

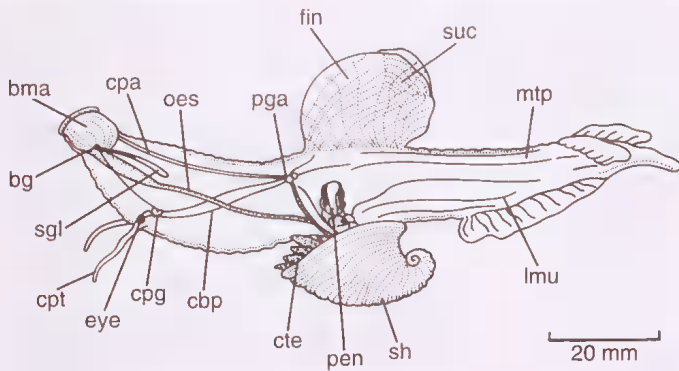


Figure 15.5 *Carinaria mediterranea* (Caenogastropoda, Carinariidae), a male heteropod in swimming position, its ventral surface uppermost. The body wall is sufficiently transparent to allow most of the contents of the head-foot to be seen except for the delicate visceral loop. The shell obscures the organs of the visceral mass, and the columellar muscles and the muscles of the head have been omitted. bg, buccal ganglion; bma, buccal mass; cbp, cerebropleural connective; cpa, cephalic artery; cpg, cerebropleural ganglion; cpt, cephalic tentacle; cte, ctenidium; eye, eye; fin, fin; lmu, longitudinal muscles; mtp, metapodium; oes, oesophagus; pen, penis; pga, pedal ganglion; sgl, salivary gland; sh, shell; suc, sucker. (After Fretter & Graham 1962) [B. Scott]

(about 10 g.mm^{-2} ; Grenon & Walker 1981), so that some other mechanism must be involved. Grenon & Walker (1981) proposed that this is 'tack', the force required to separate two closely opposed surfaces with a film of viscous liquid filling the gap. Other factors are also important, such as the properties of the mucous secretions under different tensions.

Burrowing has evolved in several groups and is associated with convergent modifications to the shell and foot. An increase in the size of the pedal sinus is associated with greater burrowing ability and a wedge-shaped foot has evolved several times, for example, in the Naticidae and Olividae as well as in some opisthobranchs (Trueman & Brown 1992). Modifications and adaptations for burrowing life in gastropods are reviewed by Trueman & Brown (1992). Modified, the foot can be used for 'surfing' or 'sailing' as in *Bullia* and *Hastula* species (Fig. 14.11; Miller, B.A. 1979).

In *Calliostoma* species and all trochids other than members of the subfamily Margaritinae, in at least some pleurotomariids (Fretter 1964) and in the genus *Haliotis* (Crofts 1929), the foot is involved in cleaning the shell in a rather unusual way. The anterior end is extended and the anterior part of the sole is firmly attached to the substratum by mucus. At the same time the posterior part of the mesopodium is extended, becoming tongue-like, and its dorsal surface then slowly wipes the shell from tip to base (Jones 1984). This action removes organic and inorganic matter; and mucus from the foot, smeared over the shell, seems to offer an unsuitable surface for settlement of epizoic organisms. The tongue-like extension of the mesopodium appears to be brought into action only for this purpose. At other times the dorsal surface of this area, which lies posterior to the opercular lobe, is folded longitudinally in the midline with its lateral edges raised to meet one another.

The pelagic, swimming heteropods have undergone considerable structural modification. The shell is lightly built, transparent, and only in the Atlantidae large enough for the animal to retract into. In the other two families, Carinariidae (Fig. 15.5) and Pterotracheidae, the head-foot has expanded to form an elongate cylindrical structure, transparent and nearly invisible in life except for the prominent eyes. Carinariids have retained a small shell sitting over the visceral mass and, on the opposite side of the body, a fin which represents the foot. In Pterotracheidae all these structures are lost.

Epipodium

An epipodial skirt is found in many Vetigastropoda and possible homologues are also found in two genera of Nacellidae (Patellogastropoda) (Powell 1973), a few Neritopsina and some cerithioideans (Houbrick 1988, 1993a). Many fissurellids have only a row of small tentacles, but the epipodium reaches its greatest development in higher vetigastropods, notably trochoideans. The development of long epipodial tentacles with sensory papillae and epipodial sense organs is a feature of vetigastropods (Haszprunar 1988a). An epipodium is generally weakly developed or absent in the cocculiniform groups (Haszprunar 1988c), although there are up to four pairs of epipodial tentacles in *Choristella* species (McLean 1992a). No adult patellogastropod has epipodial tentacles (similar structures are present in the veliger) and they are absent in most neritopsines, the exception being the genus of phenacolepadids associated with hot-vents which is reported to have small 'papillae' (Beck 1992b).

In *Calliostoma* (Fig. 15.3) and other trochoideans, the epipodial fold encircles all but the anterior margin of the foot; several epipodial tentacles arise laterally, immediately below the fold (Fig. 15.3). The broadest parts of the epipodial fold are the neck lobes, which function as inhalant and exhalant siphons for entry and exit of water. The left (inhalant) neck lobe of *Calliostoma* is papillate, but the right is smooth. Both have cilia over limited areas, but they are very dense on the antero-dorsal surface of the right (exhalant) lobe. Posterior to each lobe are four or five epipodial tentacles, each arising from a short sheath just below the epipodial fold. The epipodial (and cephalic) tentacles are covered laterally by sensory papillae.

Shell or Columellar Muscle(s)

The shell muscle in coiled gastropods is attached to the columella of the shell (hence the name columellar muscle) and runs down the concave side of the visceral hump to a ventral position slightly to the right of the body (Fig. 15.3). From there bundles of fibres pass into the head, the anterior and posterior halves of the foot and, in particular, to the opercular lobe. The majority of the fibres are dorso-ventral (parallel to the shell axis) and it is these that, on contraction, withdraw and keep the snail in the shell.

Tension in transverse and antero-posterior fibres, at right angles to the dorso-ventral ones, causes elongation of the relaxed dorso-ventral fibres so that the muscle as a whole exerts a force that pushes the foot out of the shell (Brown & Trueman 1982). Undoubtedly haemocoelic pressure also plays a part in this. In limpets the shell muscle is U-shaped and extends around much of the shell. In some coiled gastropods, the columella has ridges or folds (see Fig. 14.12) that may serve to increase the surface area for attachment of the columellar muscle (Signor & Kat 1984).

Most Gastropoda have a single shell muscle, whereas in other molluscan classes these muscles are paired. However, in many vetigastropods, patellogastropods and neritopsines they are composed of right and left muscles, even though these may be fused into a single muscle, as shown by their ontogeny (Smith, F.G.W. 1935; Crofts 1955). In higher vetigastropods and caenogastropods there is only a single shell muscle (the columellar muscle), derived from the right pretorsional mesodermal band (Crofts 1955; Werner 1955; Fretter 1969; Bandel 1982; Haszprunar 1985c). A few caenogastropods such as the velutinoideans *Lamellaria*, *Trivia* and *Velutina* (Fretter & Graham 1962) have paired shell muscles and Haliotidae are unique in that the post-torsional right muscle is the largest. Voltzow (1994) provided a detailed review of the literature on 'prosobranch' muscles.

In a few groups, such as the Patellogastropoda, Neritopsina and some Cocculiniformia, the shell muscles are divided by blood sinuses passing through them (Haszprunar 1988a).

The Shell

The orientation of the shell and the shape of the aperture relative to the head-foot have been studied in relation to efficiency of locomotion (Linsley 1978a; McNair, Kier, Lacroix & Linsley 1981). For optimum effect, a creeping aquatic snail must hold the shell such that: there is a good balance of the visceral mass over the attachment provided by the head-foot; the centre of gravity is low; minimal, or at least not too great a resistance is offered to the water and/or sediment during forward movement; and adequate space is allowed for the entry and exit of the respiratory water. These needs appear to govern much of the evolutionary change in shell shape which has occurred in streptoneuran gastropods. They are satisfied most effectively by holding the shell symmetrically over the midline of the head-foot. This is not the position in which it is held in most 'primitive' gastropods (for example, many trochoideans). Generally, the axis of the visceral mass (the axis of coiling) is inclined at an angle to the axis of symmetry of the head-foot. Linsley (1978a) described two devices which bring about the desired alignment: the axis of coiling can be lowered, and perhaps shortened so that the visceral mass lies more nearly parallel to the substratum and, by what Linsley called 'regulatory detorsion', the visceral mass is rotated clockwise slightly, bringing the two axes more nearly parallel to one another. These devices reduce drag and have the further advantage of keeping the apertural plane more or less parallel to the substratum, so facilitating the movement of respiratory water.

Linsley (1978a) interpreted much of this change in shell positioning and also changes in apertural shape as producing greater adhesion or speed. Palmer (1980) suggested this was an over-simplification of the situation and that the changes correlate equally well with other factors such as the nature of the substratum and details of the locomotor type.

The shape and size of the aperture are related to the shape and size of the foot, since this must extend and retract through it. McNair *et al.* (1981) have suggested that apertural shapes fall into three groups. Round apertures are linked to a foot with a length : width ratio of 1.1 to 1.8, found primarily in rock-clinging snails such as littorinids and some muricids. Long apertures are correlated with a long, narrow foot with length : width ratios of 3 to 4, as in cones and cowries. This arrangement allows easy travel and passage of respiratory currents, but does not afford a tenacious grip on the substratum. The group with apertures of intermediate shape appears to comprise animals of mixed habit and habitat which cannot be clearly assigned to the other groups. Vermeij (1981) correlated apertural shape with protection against predators rather than with habitat or movement.

The shape and ornament of the shell may also be broadly linked to mode of life. Limpet-shaped shells develop by very rapid expansion of the generating spiral and have evolved in many different gastropod groups (Graham 1985). Although many are adapted for clamping to the substratum, few probably evolved to resist exposure to pounding wave action as is popularly thought. A lower rate of expansion combined with a greater degree of translation of the whorls along the axis of coiling, produces a turbiniform or low conical shell, as in many trochids and littorinids. Such shells are well suited for clamping to hard substrata because the spire is nearly symmetrically placed over the attached aperture. When the translation rate is high and the expansion rate of the spiral is low, a tall, slender, conical shell is produced, with a small aperture (for example, turritellids, cerithiids, epitoniids, eulimids). Animals with these shells are not well suited either for clinging or forward movement. Such a shell is commonly dragged behind the animal as it creeps over, or burrows through, a soft substratum.

Shell ornament may be related to mode of life. Burrowing snails often have smooth shells, especially if they are globular, since this reduces frictional resistance. Other burrowers, however, more particularly some with tall shells such as some turrids and terebrids, often have ridges running round the whorls, or have costae or tubercles, all with a steep adapical end and tapered

abapical slope, which appear to act as ratchets (Signor 1983) allowing the shell to penetrate the substratum easily, but holding it in position and preventing backsliding when the foot probes forward for anchorage for the next step. Vermeij & Zipser (1986) also analysed burrowing performance in gastropods. Labial varices, thickenings, and internal teeth ornament the aperture of many epifaunal snails, often those living on hard substrata, and strengthen the shell against such predators as crabs and fishes; such ornamentation occurs in many muricids, cymatiids, and some buccinids, nassariids and rissoids (Vermeij 1978, 1979, 1982).

Epifaunal snails on soft substrata, such as some muricids and strombids, may have long spines near the aperture or, as in some xenophorids and the turbinid *Guildfordia*, peripheral spines or a flange. These devices help to spread the weight of the animal, allowing it to perch on, or move over, the surface. The production of ornament may be sensitive to changes in environmental factors. Wigham (1975) described how a European rissoid (*Rissoa parva*) living in quiet conditions produces costae whereas the same species living in exposed situations secretes smooth shells. The same animal might switch from one type of secretion to the other quickly as seasonal conditions change, whereas others, presumably genetically different, did not change their pattern. Similarly in the North Atlantic muricid *Nucella lapillus*, a variety with flange-like projections is characteristic of quiet sublittoral habitats, whereas intertidal forms have smoother shells. Largen (1971), however, found imbricate forms that bred true in littoral situations and suggested that genetic factors must also be involved (but see Palmer 1985).

Although some significant changes in shell and body form clearly can be related to major adaptive changes (for example, heteropods), often similar shell morphologies do not necessarily indicate similar life styles. For example, limpets, having a shell form often associated with wave action, can occur in high energy habitats (open coast, swift flowing rivers) or in very quiet habitats such as the deep sea or quiet ponds. Similarly, shell elongation has been suggested as a modification of the shell which offers less drag when burrowing (for example, Linsley 1978a, 1978b), but many gastropods with high-spined shells do not burrow and probably never did (for example, triphorids, cerithiopsids, many eulimids). Shell loss (resulting in a slug) has occurred in some groups, notably Opisthobranchia and Pulmonata, but is very rare in 'prosobranchs'. Semi-slugs, in which the shell is markedly smaller than the body, are found in two vetigastropod groups (Fissurellidae, Trochoidea), but no known living vetigastropod has completely lost its shell. *Titiscania* is the only slug-like neritopsine genus. Lamellariids are the only caenogastropods to adopt an essentially slug-like form, having small internal shells, and caenogastropod semi-slugs are rare, occurring in a few Naticidae. Vermiform shell-less eulimids have evolved amongst the internal parasites in that group (Warén 1983a).

Shell Structure

Shell structure is much more diverse in the more basal gastropod groups than in the more derived groups in which it is mainly aragonitic crossed-lamellar, sometimes covered by a thin, calcitic homogeneous layer (Bøggild 1930; Bandel 1990). The greatest range in shell structure is seen in patellogastropods (see also Patellogastropoda this chapter). A unique type of shell structure is found in vetigastropods (crossed-platy structure) and cone complex crossed-lamellar structures occur in patellogastropods, some vetigastropods and Neritopsina. Higher vetigastropods have lost the cone complex crossed-lamellar structure and have developed nacreous structures (Carter & Hall 1990; Hedegaard 1990).

In some patellogastropods, vetigastropods and neritopsines, both calcitic and aragonitic shell layers are present, which is presumed to be a primitive condition (Bøggild 1930; MacClintock 1967; Lindberg 1988a; Hedegaard 1990). The derived taxa have primarily aragonitic shells (either crossed-lamellar or nacre) with thin homogeneous calcitic outer layers. Unlike their relatives, littorinids living in high latitudes in both hemispheres have a calcitic shell layer (Taylor, J.D. & Reid 1990).

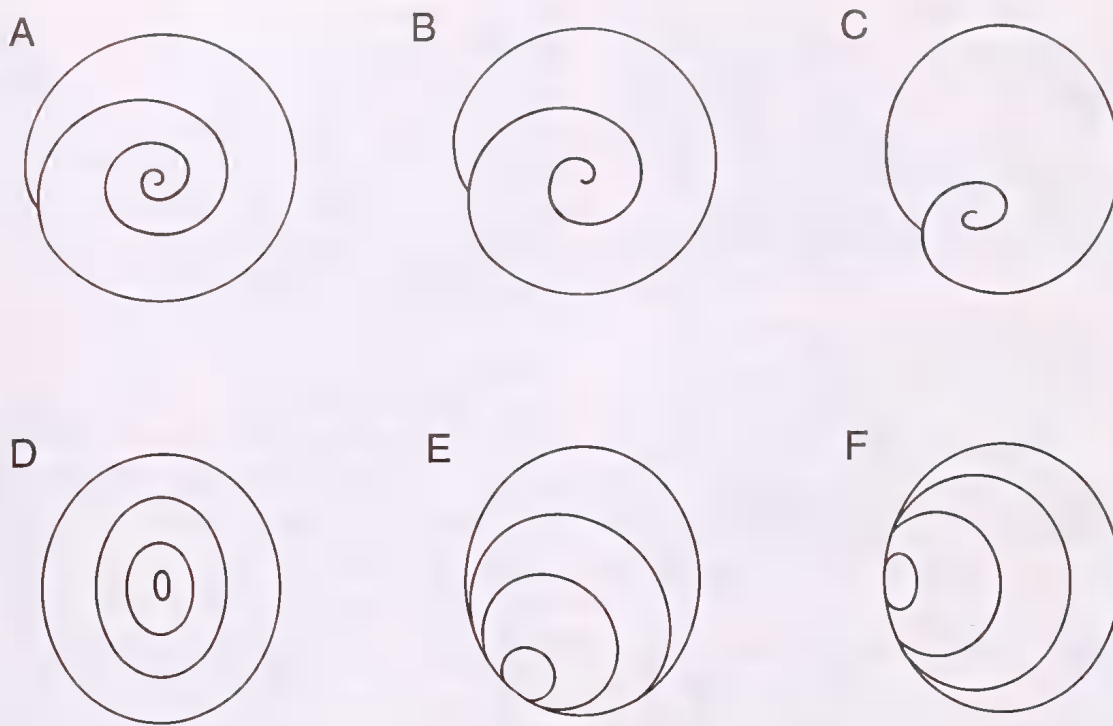


Figure 15.6 Some types of opercular coiling, viewed from outer surface. A, multispiral with central nucleus; B, paucispiral with central nucleus; C, paucispiral with eccentric nucleus; D, concentric with central nucleus; E, concentric with terminal nucleus; F, concentric with lateral nucleus. [C. Eadie]

Operculum

An operculum is present in all larval gastropods, but in many different groups it is lost in the adult. The loss is generally associated with the adoption of a limpet- or slug-like habit. The operculum is secreted by the opercular lobe and may be tightly (multispiral, as in species of *Calliostoma*) or loosely coiled (paucispiral), with the nucleus central, offset (eccentric) or marginal (Fig. 15.6). In nearly all neogastropods, the operculum (when present in adults) has lost its spiral form. Mostly the operculum is horny (corneous), but in some groups it is calcified, and markedly so in turbinids.

The Organs of the Mantle Cavity

Some vetigastropods, pleurotomariids, fissurellids, scissurellids and haliotids have a double set of organs in the pallial complex: two ctenidia, two osphradia, right and left hypobranchial glands, two auricles and two kidneys. In these respects, they show some of the bilateral symmetry characteristic of all other classes in the phylum. The coiled shell has imposed an inequality on the development of some of these organs, with the result that those belonging to the post-torsional right side are typically lost or, less commonly, smaller than their counterparts on the left. This difference is expressed in various ways in different groups of gastropods. Fissurelloidean limpets have (probably secondarily) bilaterally symmetrical ctenidia, but the right kidney is always larger than the left. McLean (1984a), Yochelson (1984) and Ponder & Lindberg (1997) suggested a relationship with this group and the extinct planispiral, bilaterally symmetrical, slit-bearing bellerophonids, a group sometimes not (probably wrongly) regarded as gastropods. Most gastropods have lost the right ctenidium; some patellogastropods (Patelloidea) have given up the use of the mantle cavity altogether as the primary respiratory space and developed secondary gills outside it.

In vetigastropods with two ctenidia, each usually consists of an axis bearing a row of respiratory lamellae on each side. Anteriorly (Fig. 15.7B), the axis lies freely in the mantle cavity, but posteriorly (Fig. 15.7A) it is held by two membranes running to the mantle skirt: the afferent membrane dorsally, and the efferent membrane ventrally. The afferent membrane provides a support for vessels bringing blood to the ctenidium, the efferent

membrane bears vessels leaving it. The antero-posterior extent of each membrane appears to be a compromise between the need for support for the ctenidium and interference with the flow of respiratory water which it necessarily produces. The mantle cavity is thus divided as far as the membranes extend, into three compartments (Fig. 15.7A), a lateral one on each side, each with one set of gill lamellae, and a central one, containing two sets of lamellae, one from each ctenidium. Water enters the mantle cavity on the left and on the right, washes over the corresponding osphradium and ctenidium, and the two streams converge in the central compartment, into which the anus and the two kidneys discharge. This part therefore forms a cloacal chamber and the efficient removal of its contents has been solved in different ways in different groups. Pleurotomarioideans and fissurelloideans nearly all have special exhalant openings in the shell (Fig. 15.7C), though these may also help in allowing entry of water (Murdock & Vogel 1978; Voltzow 1983).

Chitinous skeletal rods are present in the ctenidia of most vetigastropods, caenogastropods and hot-vent taxa, but are absent from patellogastropod and neritopsine ctenidia, a condition thought to be primitive (Salvini-Plawen 1981; Haszprunar 1988a).

Although *Calliostoma* species and other trochids have only a single left ctenidium (Figs 15.7D, 15.8) and osphradium, the rectum and anus (Fig. 15.8) towards the right are bordered by left and right hypobranchial glands and left and right kidney openings. The right kidney opening in the female is more anteriorly placed than that of the male. The ctenidium extends the length of the mantle cavity (Fig. 15.8). It consists of an axis carrying a right and left series of leaflets (filaments) for more than a third of its length anteriorly, but only a single row, the right, posteriorly. The anterior third of the ctenidium is free and its axis on the afferent side is covered by a sensory epithelium, the osphradium. Posterior to this free part, the axis is fastened by a narrow suspensory membrane to the side of the mantle cavity laterally and to the mantle skirt above (Fig. 15.7D). The filaments on the right project into the main mantle cavity, whereas those on the left are cut off from the main cavity by the suspensory membrane and lie in a small, short, separate cavity. Behind this cavity, there are no leaflets on the left and the axis fuses with the mantle skirt. Near the efferent border of each filament, as in other vetigastropods, there is a slit-like opening to a sense organ, the bursicle.

15. PROSOBRANCHS

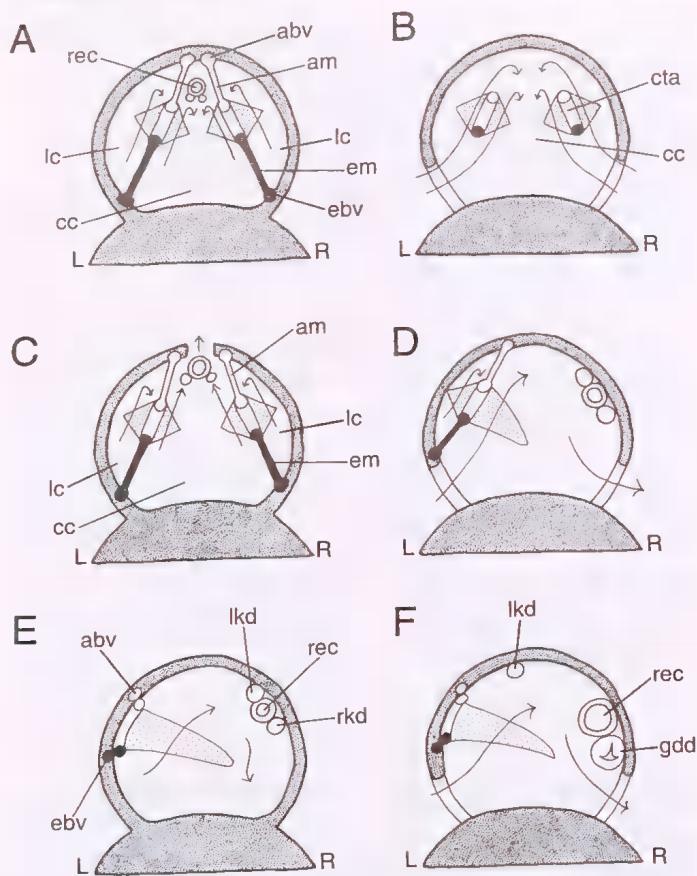


Figure 15.7 Diagrammatic transverse sections through a series of gastropods to illustrate the organisation of the mantle cavity in relation to water flow through it. A, B, hypothetical ancestral vetigastropod: A, at level of posterior mantle cavity; B, at level of anterior mantle cavity. C, pleurotomarioidean or fissurelloidean (dibranchiate vetigastropod) near posterior end of mantle cavity. D, E, trochoidean (monobranchiate vetigastropod): D, at level of anterior mantle cavity; E, at level of posterior mantle cavity. F, caenogastropod. Arrows show the direction of the water currents. abv, afferent branchial vessel; am, afferent membrane; cc, central compartment of the mantle cavity; cta, ctenidial axis; ebv, efferent branchial vessel; em, efferent membrane; gdd, genital duct, incorporating the right kidney in caenogastropods; L, left side of animal; lc, lateral compartment of mantle cavity; lkdk, left kidney duct; R, right side of animal; rec, rectum; rkd, right kidney duct. [B. Scott]

The ctenidial leaflets are triangular, with their bases fused to the axis. The bipectinate condition, although found in most vetigastropods, including trochids like *Calliostoma*, has been lost several times in the Trochidae (Haszprunar 1993).

The efferent branchial vessel (Fig. 15.8) runs along the left edge of the axis and posteriorly enters the pericardial cavity which is situated transversely at the base of the visceral mass (Fig. 15.8). The afferent branchial vessel runs along the right edge of the ctenidial axis and draws blood from vessels traversing the left hypobranchial gland (Fig. 15.8). The leaflets contain a network of spaces through which blood travels from afferent to efferent vessel, with the latter facing the incoming water flow, thus producing a counter-current system. Cilia on the leaflets drive a current of water through the mantle cavity from left to right. The main (lateral) cilia lie near the efferent margin overlying the skeletal rod. Small particles brought into the mantle cavity by the inhalant stream are bound in the mucus of the hypobranchial gland and are swept out of the mantle cavity, via the right neck lobe, along with excretory and faecal matter.

The loss or reduction of pallial organs on the right side, resulting in a left-right water flow, has occurred independently in trochoideans, neritoideans, patellogastropods, caudofoveate limpets, the hot-vent groups and in caenogastropods (Yonge 1947; Salvini-Plawen 1980; Haszprunar 1988a; Ponder & Lindberg 1996); an intermediate condition showing considerable reduction is found in some Vetigastropoda, and Neritopsina (Haszprunar 1988a). However, caenogastropods differ from the

other non-heterobranch groups in having lost all post-torsional right pallial organs. They have a single (left) ctenidium and osphradium, like the other groups, but they have only a single hypobranchial gland, auricle and kidney, although a rudiment of the right kidney is incorporated in the reproductive system. Also, unlike that of most members of other 'prosobranch' groups, the caenogastropod ctenidium is monopectinate, consisting only of the left set of lamellae; there is no trace of the ctenidial membranes, and the ctenidial axis fuses to the mantle skirt (Fig. 15.7F). Within the caenogastropod mantle cavity, therefore, only that section corresponding to the vetigastropod cloacal chamber remains, enlarged by a rightward migration of the rectum and anus. It is divided by the gill lamellae into a ventral (sub-branchial) inhalant, respiratory part connected to the external environment on the left, and a dorsal (suprabranchial) exhalant, cloacal part connected to the external environment on the animal's right. These changes transform the current ventilating the mantle cavity into a single left-right stream (Figs 14.16B, 15.7D–F). Though morphologically equivalent to the archaeogastropod cloacal chamber, the 'cloacal' nature of the suprabranchial chamber has been reduced by the anterior extension of the rectum so the anus opens near the right edge, rather than in its depths. However, the left kidney discharges posteriorly in most caenogastropods.

Ctenidial modifications associated with suspension-feeding have evolved independently in vetigastropods, caenogastropods and in the hot-vent genus *Neomphalus*. In caenogastropods, a glandular strip (endostyle) providing mucus has evolved independently in some cerithioideans (Turritellidae) and neotaenioglossans (for example, Struthiolariidae, Calyptraeidae; Fig. 15.9), but this is not found in suspension-feeding Umbonionae (Trochoidea) (Fretter 1975; Hickman & McLean 1990) or in *Neomphalus* (Fretter, Graham & McLean 1981).

The rectum in caenogastropods (Fig. 15.7F) and neritoideans lies on the right instead of more or less centrally as in vetigastropods and patellogastropods. In both groups, this space is shared with a glandular genital duct developed, in caenogastropods, from the original right hypobranchial field. There is a prostate gland in males, and females have glands that produce albumen and material to make protective coverings for fertilised eggs. These glands allow a reproductive mode other than the broadcasting of gametes practised by many vetigastropods and patellogastropods and are essential preadaptations for the invasion of freshwater and terrestrial habitats. The 'prosobranch' mantle cavity, although being well suited to life in freshwater, requires considerable modification for life on land. In all terrestrial taxa the gills, and in most the hypobranchial glands and osphradia are lost and there are also modifications to the kidney, as described below.

Alimentary Canal, Digestion and Feeding

The overall trend in the gastropod alimentary canal is one of increasing simplification (Stuber & Lindberg 1989), although some increasing complexity is seen in the foregut, notably in those taxa with a proboscis and accessory foregut glands. In the account below, we examine some of the trends seen in the digestive system of streptoneuran gastropods, commencing with a description of the digestive system of *Calliostoma*.

Ancestral gastropods rasped and scraped their food with a radula worked by a complex musculature associated with the odontophore. The food was probably largely detrital and must have included live and dead plant and animal material. Digestion took place in the stomach in the presence of enzymes from the oesophageal and digestive glands. Digested food entered the cells of the digestive gland and perhaps also those of the intestinal epithelium while the residual material was compacted by intestinal secretions to form faecal rods or pellets.

There is evidence that, at least in intertidal species, feeding and digestive activity are cyclical (Merdsoy & Farley 1973; Bogen & Farley 1974; Wigham 1976).

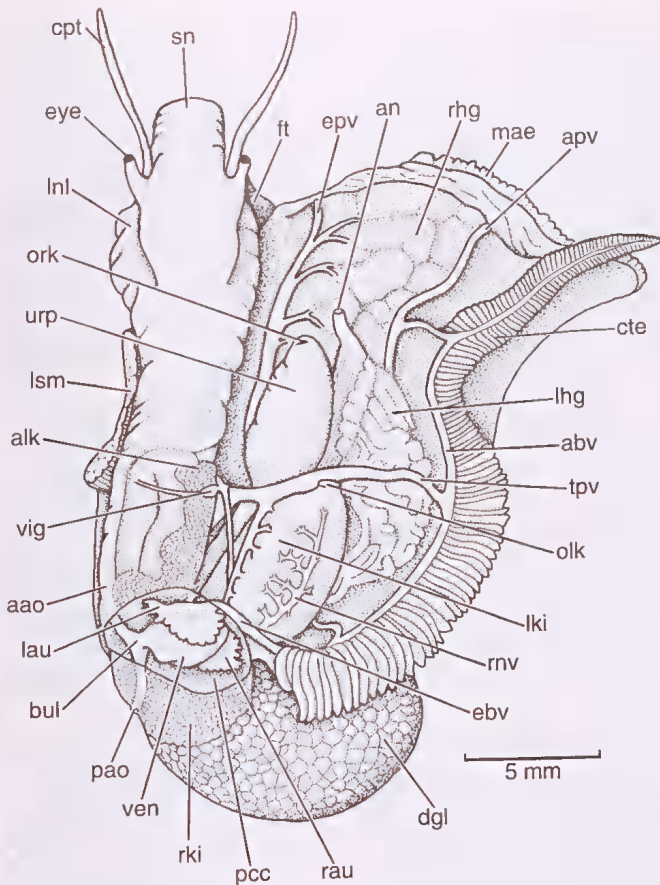


Figure 15.8 A female *Calliostoma zizyphinum* (Vetigastropoda, Trochidae) dissected to show the vascular system in the mantle skirt and the organs of the mantle cavity; some other organs are seen by transparency. aao, anterior aorta; abv, afferent branchial vessel; alk, anterior lobe of right kidney associated with anterior loop of intestine; an, anus; apv, anterior pallial vein; bul, bulbus aortae; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; ebv, efferent branchial vessel; epv, efferent pallial vein; eye, eye; ft, foot; lau, left auricle; lhg, left hypobranchial gland; lki, left kidney (papillary sac); lnl, left neck lobe; lsm, left shell muscle; mae, mantle edge; olk, opening of left kidney; ork, opening of right kidney (urinogenital); pao, posterior aorta; pcc, pericardial cavity, opened; rau, right auricle; rhg, right hypobranchial gland; rki, right kidney; rnv, renal vessel connecting with efferent branchial vessel and associated with nephridial gland (adjacent stippled area); sn, snout; tpv, transverse pallial vein; urp, urinogenital papilla; ven, ventricle; vig, visceral ganglion. (After Fretter & Graham 1962) [B. Scott]

Digestive System of *Calliostoma*

Until comparatively recently, it was thought that *Calliostoma* species are herbivores and detritivores like many other members of the Trochidae. However, it is now known that the diet of six species, all living in the Northern Hemisphere, includes at least some tissues of cnidarians, including hydroids and soft corals.

In *Calliostoma* species and other trochids, the oral edge of the large snout is fringed with papillae (Fig. 15.3) which surround the radially folded lips. The lips are split mid-ventrally and extend posteriorly on the right into an elongate flap which is rolled to form a pseudoproboscis (Fig. 15.3) of unknown function and found only in a few other vetigastropods.

Food is gathered by means of the buccal mass and odontophore, a tongue-like elevation of the buccal floor consisting of a complex mass of muscles attached in part to skeletal 'cartilages', and in part to the body wall (Figs 14.22A, 15.10). The odontophore can be moved in and out of the mouth as the animal feeds. In *Calliostoma* species and many other vetigastropods each half of the odontophore has an anterior and a posterior cartilage, closely interlocked. Between them, over the mid-dorsal surface, runs the radula, a ribbon of chitin-bearing teeth in regular longitudinal and transverse rows (see for example, Figs 15.56C, 15.65E).

Caenogastropods have a single pair of cartilages and in Patellogastropods there are two to five pairs. In the resting odontophore, and within the radular sac, the radula is folded into a cylinder and the cusps of all the teeth point inwards. As the odontophore is moved in and out of the mouth, the radula is moved backwards and forwards by the complex musculature (see Fig. 15.10) over the angled edge of its tip. On the outward thrust, when the odontophore tip curves ventrally, the lateral and marginal teeth spread sideways at this edge, their movement being regulated by the jaws, whereas on retraction they are folded in towards the midline. Thus, during feeding, when the radula is continually moved forwards and back, the teeth spring from one position to the other. On the inward movement they are directed towards the midline as the curved cusps gather food from the substratum and draw it through the mouth into the buccal cavity. The process is lubricated by secretions from a pair of salivary glands which open to the buccal cavity on each side of a dorsal ciliated food channel. Protrusion of the odontophore is brought about by muscles originating on the anterior part of the buccal wall and inserted posteriorly on the cartilages. When these muscles relax the odontophore returns to the resting position.

The radula is retracted by the action of stout muscles originating on the posterior ends of the cartilages on each side and inserted laterally on the radular membrane. The dorsal food channel leads posteriorly to the oesophagus beneath which is the opening of the radular sac (Fig. 15.10). These two openings are separated by the flap-like oesophageal valve, which closes the opening to the dorsal food channel to prevent regurgitation of food when the odontophore protrudes and, on its withdrawal, closes the opening to the radular sac.

The radular teeth are formed at the inner end of the radular sac which extends well beyond the posterior end of the odontophore and ends blindly. As the teeth are gradually moved forward along the sac, they are hardened and tanned by secretions from the supra-epithelium. They pass on to the surface of the odontophore as those already there are lost or broken. The epithelium of the capacious buccal cavity is cuticularised, except postero-dorsally and anteriorly, forming lateral jaws (Fig. 15.10) composed of numerous small rods. The jaws may assist in manipulating the radula as well as in feeding.

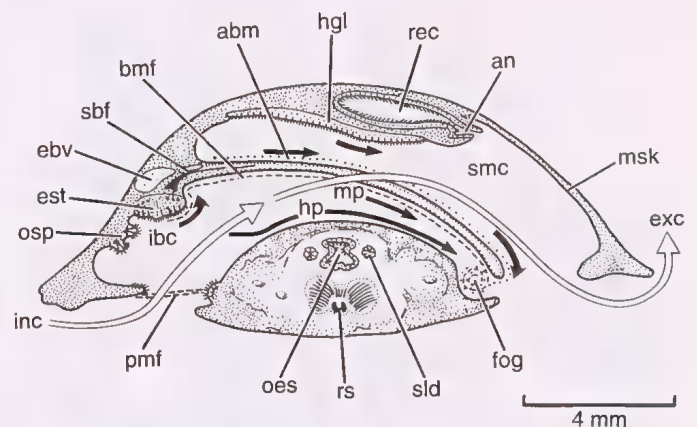


Figure 15.9 Feeding and respiratory currents of *Crepidula fornicata* (Caenogastropoda, Calyptraeidae). Transverse section of mantle cavity showing the direction of water currents (continuous arrows) and ciliary currents (broken arrows). abm, abfrontal mucous stream; an, anus; bmf, branchial mucous filter collecting fine particles; ebv, efferent branchial vessel; est, endostyle; exc, exhalant current; fog, food and mucus string in food groove; hgl, hypobranchial gland; hp, course followed by heavy particles; ibc, infrabranchial part of mantle cavity; inc, inhalant current; mp, course followed by medium-sized particles; msk, mantle skirt; oes, oesophagus; osp, osphradium; pmf, pallial mucous filter collecting coarse particles; rec, rectum; rs, radular sac; sbf, skeleton in branchial filament; sld, salivary duct; smc, suprabranchial part of mantle cavity. (After Fretter & Graham 1962) [B. Scott]

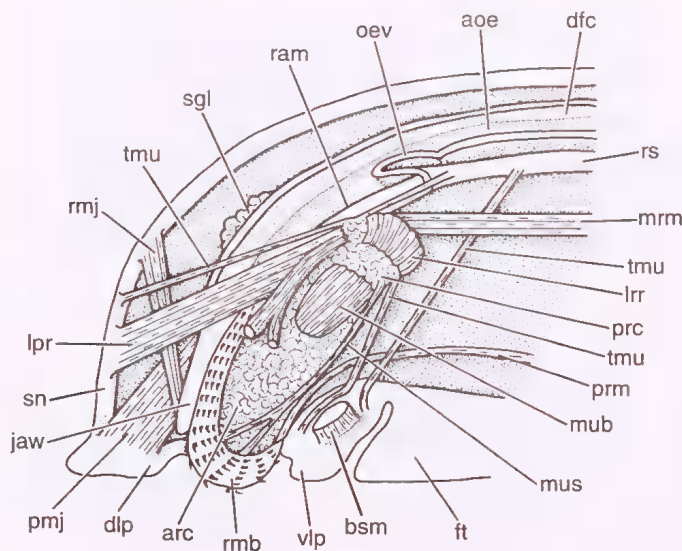


Figure 15.10 Trochid head dissected from the left side to show the organisation of the front end of the gut. The odontophore is protruded, and its tip applied to the substratum; only the main muscles related to its protrusion and withdrawal are indicated. The left half of the radular membrane has been removed to display the cartilages. The nervous system is omitted. aoe, anterior oesophagus; arc, anterior radular cartilage; bsm, buccal sphincter muscle (cut); dlc, dorsal food channel; dlp, dorsal lip; ft, foot; jaw, jaw; lpr, lateral protractor muscle of odontophore; mrm, median retractor of radular membrane passing to columellar muscle; mus, muscle spreading radular membrane on protrusion of odontophore; oev, oesophageal valve; pmj, protractor muscle of jaw; pnc, posterior radular cartilage; prm, protractor of radular membrane passing to columellar muscle; ram, infolded radular membrane; rmb, radular membrane opened out with teeth erect; rmj, retractor muscle of jaw; rs, radular sac; sgl, salivary gland; sn, snout; tmu, tensor muscle; vlp, ventral lip. (Modified after Fretter & Graham 1962) [B. Scott]

The oesophagus of *Calliostoma* species and other trochids connects the buccal cavity with the stomach situated in the visceral mass and is divisible into three sections: the anterior oesophagus (Fig. 15.10) lies directly behind the buccal cavity and anterior to the area affected by torsion; the mid-oesophagus, which includes the length involved in torsion; and the posterior oesophagus, which opens to the right wall of the stomach. The epithelium of the anterior oesophagus is ciliated and glandular and the two dorsal folds, continuous with those in the buccal cavity and separated by the deep dorsal food channel, extend along it and continue into the mid-oesophagus. To right and left of the ventral midline, two separate ridges termed ventral folds arise behind the oesophageal valve and also continue posteriorly. These folds are absent in caenogastropods. Laterally, the walls are drawn out into pouches which communicate widely with the rest of the cavity and provide space for the accommodation of food during feeding and may also ease the movements of the buccal mass and radula. These pouches are also typically absent in caenogastropods. The lateral walls of the mid-oesophagus of *Calliostoma* species are greatly expanded to form the oesophageal glands. The internal surface area is increased by the development of finger-like outgrowths, peculiar to vetigastropods, which are covered by a glandular epithelium. These glands produce the first digestive secretion which the food meets, as the saliva is devoid of digestive action.

The effect of torsion on the mid-oesophagus can be seen by tracing the course of the dorsal food channel – morphologically, the mid-dorsal line – over the left side until it comes to lie in the topographically mid-ventral line. Simultaneously, the ventral folds curve round the right side until they lie in the topographically mid-dorsal line. The glandular areas also cross to lie on the side opposite to that on which they originally occurred. The anterior limit of the area affected by torsion is marked by the supra-oesophageal part of the visceral nerve loop. Its posterior limit is shown by the anterior aorta which curves over the oesophagus from a dorsal position on the left, where it emerges from the heart, to a ventral position on the right, where it divides into cephalic and pedal branches. The median part of the mid-oesophagus is converted into a virtually closed channel by the ventral folds interleaving with the dorsal folds.

The cilia on the walls of the food channel beat in the direction of the stomach and mucus secreted from the channel's epithelium binds the food particles and lubricates their passage. Over the summit of the folds the direction of the ciliary beat is transverse, from the lateral glands to the food channel and this, together with ciliation on the glandular villi and muscular activity in the walls of the glands, brings their secretion to the food channel to be mixed with the food as it is transported along the simple posterior oesophagus to the stomach.

The stomach is an ovoid sac embedded in the digestive gland near the base of the visceral hump on the left (Fig. 15.3). It is divisible into a more posterior globular part from which a spiral caecum arises posteriorly, and a more cylindrical anterior part, the style sac, opening to the intestine (Fig. 15.11). The oesophagus opens near the posterior end of the stomach to a groove on its right wall into which the single duct of the digestive gland also discharges. This groove, bounded by a deep fold along its left side, runs into the mouth of the spiral caecum. On reaching the blind end of the caecum it recurves on its course, expanding as it returns.

Within the caecal groove food and enzymes from the oesophageal glands and digestive gland are mixed with mucus, consolidated and spun into a thread. On leaving the caecum this piles up between the gastric shield, a heavily cuticularised area of the gastric epithelium, and, on the opposite wall, the duct of the digestive gland. Ventrally, between these two areas and extending to the mouth of the caecum, vigorous ciliary currents sort, on the basis of size, particles falling from the food string. The food is squeezed by the gastric muscles against the cuticular gastric shield which offers extensive protection against abrasion. Fluid and fine particles pressed from the food mass enter the digestive gland duct

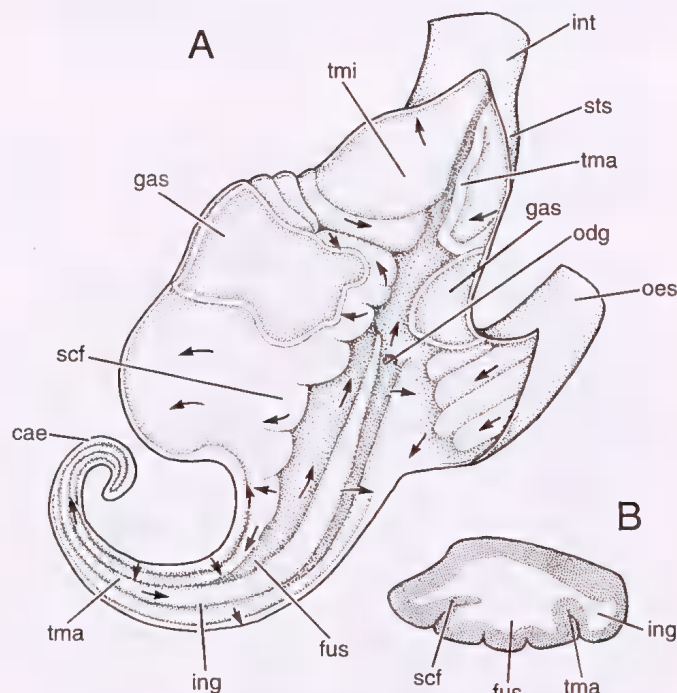


Figure 15.11 Stomach of *Calliostoma zizyphinum* (Vetigastropoda, Trochidae): A, stomach dissected by a dorsal longitudinal slit; B, transverse section of the spiral caecum. cae, spiral caecum; fus, area representing fusion of intestinal groove and sorting area; gas, gastric shield; ing, intestinal groove; int, intestine; odg, opening of duct of digestive gland; oes, oesophagus; scf, fold emerging from spiral caecum; sts, style sac; tma, major typhlosole; tmi, minor typhlosole. (After Graham 1949) [B. Scott]

and pass into tubules within the gland where they are taken up by the absorbing cells. The remainder is gradually moved forward to the style sac and waste from the digestive gland is incorporated in it. Within the style sac the waste matter is rotated by ciliary currents, and cilia on the glandular longitudinal folds (typhlosoles) move it into the intestine where it is cemented into a faecal rod of firm gelatinous consistency.

In *Calliostoma*, and in other vetigastropods, the intestine passes forwards towards the head, then bends abruptly back towards the stomach, moves to the right and runs through the ventricle of the heart before passing on to the mantle skirt as the rectum, and opening at the anus (Fig. 15.8). During development the rectum lies ventral to the heart, but the ventricle wraps round it as growth occurs. The intestine is ciliated and glandular and within it the faecal rod manufactured in the style sac undergoes further cementing and compacting before extrusion.

The digestive gland fills the main part of the visceral hump except when the gonad ripens. It is a mass of branching tubules bathed in blood in the visceral haemocoel and, in *Calliostoma* species, is composed of two lobes, each associated with a single ciliated duct. The ducts unite before reaching the stomach. The epithelium of the digestive gland comprises two types of cell. Tall columnar digestive cells are the more numerous. They contain highly vacuolated cytoplasm and have the distal border covered with microvilli. These cells take up particulate food into vacuoles, digesting it intracellularly, and also take in nutrients in solution. The products of digestion may be stored or passed into the haemocoel; the waste is extruded from the cell surface. The second type of cell is less numerous and tends to occur in groups in crypts located at the angles of the tubules. The cytoplasm in these cells is dense and stains darkly; the nuclei are large and basal. There is no evidence that these cells carry out intracellular digestion. Their morphology, with tapering distal ends and broad bases abutting the blood spaces underlying the tubules, suggests that they are involved in uptake of material from the blood; they are probably secretory. Both types of cell seem able to manufacture secretion, presumably not identical, the more numerous digestive cells being the likely source of digestive enzymes. These same two basic cell types are found in the digestive glands of other streptoneuran gastropods, even though several further types have sometimes been recognised (see review by Voltzow 1994).

Snout and Proboscis

Most gastropods have a simple snout (as in *Calliostoma* species), which is usually extensile to some extent, although in some non-probosciform caenogastropods it can extend for several times its resting length (see Ponder 1994a). The snout is sometimes referred to as a proboscis, but we prefer to restrict this term to the various types of introvert. A proboscis is formed from the invagination of the snout and several types have evolved in different caenogastropod groups (Amaudrut 1898; Fretter & Graham 1962; Ponder 1973a; Miller, J.A. 1989; Kantor 1990a, 1991, 1996), associated with carnivory. Two main types are recognised: the acrembolic form, in which the proboscis is turned outside in to produce an introvert when not in use (Fig. 15.12A, B) and the retractors are inserted at the tip of the proboscis; and the pleurembolic proboscis in which the basal half is similarly inverted to form a sheath into which the distal half may be pulled (Fig. 15.12C, D) and the retractor muscles are inserted in the middle of the proboscis (Fretter & Graham 1962). A third type, the intraembolic proboscis, in which the buccal mass is at the base of the proboscis and elongation is achieved by the oral tube, is the basic type in the Conoidea (Ponder 1973a; Miller, J.A. 1989; Kantor 1990a, 1996), but is also seen in a few other neogastropods (Kantor 1991). Kantor (1990a) has shown, on the basis of detailed differences in the musculature, that the pleurembolic proboscis evolved independently in the Tonnoidea and Neogastropoda, and he advocates independent evolution of the proboscides of all major groups of marine predatory gastropods. The neogastropod proboscis form may have evolved independently in several clades

(Ponder 1973a; Kantor 1991) and a range of proboscis types have been described, especially in the Conoidea (Smith, E.H. 1967a; Miller, J.A. 1989; Kantor 1990a, 1991).

Jaws

Patellogastropods have a jaw composed of dorsal and lateral elements. The plesiomorphic state for orthogastropods is a single pair of dorso-lateral jaws. Cocculinids have a single vestigial dorsal jaw (Haszprunar 1987a). Neritids lack a definite jaw, as do neogastropods (Ponder 1973a), with the exception of muricids (Carriker 1943; Wu 1965).

Two different types of jaw are found in gastropods – those composed of homogeneous material and those composed of small rod-like elements (Ponder & Lindberg 1997). The latter are found in most gastropods except patellogastropods and cocculinids which have homogeneous jaws, as in the members of other classes.

The Radula

In nearly all streptoneuran gastropods the radula is the major organ for the collection of food, and has been lost mainly in those which have adopted a suctorial method of feeding (for example, most eulimids and some neogastropods).

The so-called docoglossate patellogastropod radula (Figs 1.14A, 15.34) is considered to be unique in gastropods in its function (Ankel 1936a; Fretter & Graham 1962); this primitive condition has been termed stereoglossate by Salvini-Plawen (1988). In all other gastropods the radula bends longitudinally (Golikov & Starobogatov 1975), enabling the marginal teeth to sweep inwards, a condition called flexoglossate. These different radular types are reflected in different feeding movements of the odontophore and radula and, consequently, in buccal mass musculature (Fretter & Graham 1962).

The docoglossate or stereoglossate radula of patellogastropods is similar in several ways to the radulae of chitons and monoplacophorans (Golikov & Starobogatov 1975; Lindberg 1986a; Salvini-Plawen 1988). The number of teeth per row is small, with a wide attachment to the radular membrane. The teeth do not become erect when they move over the tip of the

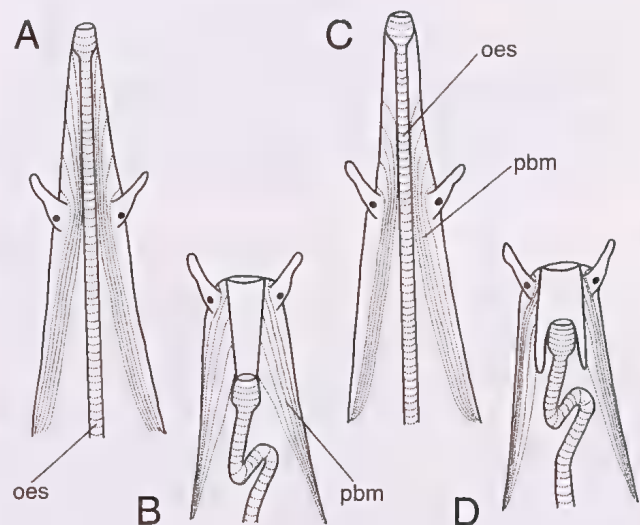


Figure 15.12 The mechanism of proboscis extension and withdrawal in caenogastropods. A, acrembolic proboscis extended. B, acrembolic proboscis withdrawn, forming an introvert. C, pleurembolic proboscis extended. D, pleurembolic proboscis retracted, its basal half then infolded to form a proboscis sheath into which its distal half is withdrawn without introversion. The proboscis retractor muscles are shown, originating on the body wall proximally and on the whole length of the wall of an acrembolic proboscis distally, but on the basal half only of a pleurembolic one. The course of the oesophagus is indicated and shows how it loops on withdrawal of the proboscis. oes, oesophagus; pbm, proboscis retractor muscles. (After Fretter & Graham 1962) [B. Scott]

15. PROSOBRANCHS

odontophore. Many are applied to the substratum simultaneously, and all act in the same longitudinal direction like a rasp instead of at an angle to the substratum, as in other types of gastropod radulae (Ankel 1938). Further, their hardness is increased by the incorporation of iron and silicon compounds (Runham, Thornton, Shaw & Wayte 1969), though some caution appears necessary in deciding whether hardness is attributable solely to these components or to the matrix (Vincent 1980).

One form of flexiglossate radula is the rhipidoglossate type, with many teeth in each row (Figs 1.14B, 15.54K, L). This is not the most primitive gastropod radula, perhaps even within the orthogastropods, although this is often assumed to be so. It is an efficient food-gathering mechanism, but does not usually have great excavating power, although there are some exceptions, particularly among neritopsines. This type of radula is found in vetigastropods, neritopsines and some caudofoveate limpets, as well as in a few valvatoidean heterobranchs (Warén, Gofas & Schander 1993). Each tooth row has, on each side of a central (= rachidian) tooth, a fan of teeth which can be divided into several (usually four or five) typically moderately stout laterals with sharp denticles, the outermost often markedly larger, and an array of fine marginals. With reduction in the number of teeth in each row (see below) the breadth of substratum covered is decreased and the excavating or rasping power is increased. Rhipidoglossans ingest primarily diatoms, and filamentous and foliose algae (Steneck & Watling 1982) and their radula makes little impression on the tougher tissues of fucoids and coralline algae. Taenioglossans, such as littorinids with only seven teeth in each row (Figs 1.14C, 15.83G), also show a preference for smaller, softer algae (Watson & Norton 1985), apparently being unable to remove tougher algae. The power necessary to deal with the toughest food cannot be attained with any radula working on the principle of the rhipidoglossate or taenioglossate type. It can be achieved, however, by the stereoglossate radula which works on a different principle.

In many gastropod lineages, the radula has undergone oligomerisation (Steneck & Watling 1982). A number of teeth in each row, particularly in those most marginally placed, are progressively lost so that the radula becomes narrower. The taenioglossate radula (seven teeth per row) is the standard pattern in the neotaenioglossan and architaenioglossan gastropods (see Fig. 1.14C). This type of radula has a single lateral and two marginal teeth on each side of a central tooth. In rachiglossate neogastropods, which all have a proboscis, the number of teeth per row is reduced to three (central + two laterals; Figs 1.14D, 15.157A–C) or one (the central). In toxoglossans, primitively there are five teeth in each row (as in some turrids), but ultimately a pair of marginals, although functionally these operate as a single tooth (see Fig. 1.14E; Ponder 1973a; Shimek & Kohn 1981; Kantor 1990a; Taylor, J.D., Kantor & Sysoev 1993).

The detailed adaptations of radular tooth structure to their precise role in feeding are too numerous to cover here (for further detail see Hickman 1980, 1984c; Voltzow 1994; see also Chapter 14). The radular tooth acts by being drawn obliquely and briefly across the substratum. Its leading surface is therefore subject to a tensile force, its attachment to the radular membrane to bending, and its back to compression. The base is usually strengthened by being expanded and the rear face by development of a longitudinal ridge; less commonly, the leading face is altered. In the original state, each tooth presumably moved independently, but in some radulae efficiency has been improved by devices which interlink neighbouring teeth. These may involve modifications of their bases, shafts, or less commonly the tips of the cusps. Consequently, the teeth may be strengthened, the stresses acting on them spread and their movement coordinated.

The power of the herbivore radula depends in part on the size of the animal, and the food ingested varies accordingly. Thus Vahl (1971) has shown that although adults of the European limpet *Helcion pellucidum* (cited as *Patina*) feed on laminarians, its young are unable to do so because the radula and odontophore are too weak. They settle on, and eat softer algae until they reach a

shell length of 4 mm and then move to the tougher laminarians. Many small taenioglossans such as rissoids (Fretter & Manly 1979) or hydrobiids (Newell 1965) scrape off the microalgae and bacteria living on larger plants or attached to sand grains. Jensen & Siegmund (1980) have shown that diatoms rather than bacteria in the epiphytic material constitute the main food item of the European estuarine hydrobiid snails *Hydrobia ulvae*, *H. neglecta* and *H. ventrosa*, and they also provide food for the neritoidean *Theodoxus fluviatilis* (Skoog 1978). Some hydrobiids use the radula in an unusual way (Fenchel 1975): they take sand grains into the buccal cavity, clean adherent micro-organisms from them with the radula, and then spit out the grains, a process which Lopez & Kofoed (1980) called epipsammic browsing.

A radular caecum (or radular diverticulum) is found in a number of 'lower' gastropods (Salvini-Plawen 1988). It is a pouch of the antero-dorsal radular sheath which lies between the radular sheath and the oesophagus.

Next to the shell, the radula provides the most accessible character complex in gastropods. Stemming from major studies such as those of Gray (1853), Troschel (& Thiele) (1856–1893), MacDonald (1860, 1880) and Thiele (1929–1935), it has been significant in higher classification, as reflected in names like Rhipidoglossa, Stenoglossa, Rachiglossa, Architaenioglossa, Toxoglossa, Taenioglossa and Ptenoglossa.

The radular sac of chitons and most gastropods is usually straight, but in many caenogastropods it is turned up markedly in a spiral coil behind the buccal mass, reaching its extreme development in the Littorinidae. The posterior end of the radular sac is simple in most gastropods, but in possibly all vetigastropods it is distinctly bifid.

Odontophoral Cartilages

Graham (1973) and Wingstrand (1985) found a common basic plan in the musculature of the odontophore of polyplacophorans, monoplacophorans and gastropods. These complex muscles differ in detail between major groups and no doubt a number of these characters will eventually be found to have phylogenetic significance (Ponder & Lindberg 1996).

The supporting cartilages in the odontophore vary from one to five pairs. The plesiomorphic condition may be either one or two pairs of cartilages (Ponder & Lindberg 1997) with multiplication and reduction in the various groups. The lower vetigastropods have three pairs of cartilages, the third pair being formed by the subdivision of one of the original pairs. Higher vetigastropods have two pairs, a reduction perhaps due to heterochrony. Caudofoveates have a single pair of cartilages (Haszprunar 1987a, 1988c), as do caenogastropods.

Salivary Glands

Most gastropod salivary glands open dorsally to the buccal cavity. Vetigastropods usually have ductless, tuft-like salivary glands, patellogastropods have ducted salivary glands and those of caenogastropods are usually tubular or ducted. Salivary glands are absent in the Neritoidea and Cocculinidae (Fretter 1965; Haszprunar 1987a).

As a result of the migration of the nerve ring behind the buccal mass, and elongation of the salivary glands, the salivary ducts either pass through the nerve ring (most neotaenioglossans) or over it (neogastropods, rissoidaeans, some cerithioideans).

Different types of accessory salivary glands are found among gastropods (Fretter & Graham 1962). The particular forms found in several groups of neogastropods are the best known and provide apomorphies for those groups (Ponder 1973a; Andrews, E.B. 1991). The secretions from these glands can contain pharmacologically active constituents (Andrews, E.B., Elphick & Thorndyke 1991), including a toxin used to paralyse prey. The accessory glands seen in some tonnoideans are not homologous with the neogastropod accessory salivary glands, being derived from the salivary duct near its origin from the main salivary gland (Fretter & Graham 1962).

Buccal Pouches

Small sacs with narrow openings open into the posterior buccal cavity in some taxa. These have been described for few caenogastropods, for example, Cyclophoridae and Ampullariidae (Amaudrut 1898), Littorinidae (Fretter & Graham 1962), Eatoniellidae (Ponder 1968a) and *Campanile* (Houbrick 1981a). Ponder (1983a) advanced the idea that, at least in some neotaenioglossans, they could be derived from the anterior part of the oesophageal gland. Certainly, in some neotaenioglossans, anterior pouches associated with the most posterior part of the buccal cavity and the anteriormost part of the oesophagus (for example, *Provanna*, Warén & Ponder 1991), are histologically similar to the oesophageal gland. In most of the other groups, the buccal pouches differ histologically from the oesophageal gland and may be buccal in origin. Whether these latter structures are homologous across the groups in which they occur is unknown.

Oesophagus and Oesophageal Glands

Typically, three regions can be recognised in the oesophagus (see Voltzow 1994). The anterior oesophagus begins at the posterior end of the buccal cavity (Fig. 15.10) and extends into the mid-oesophagus. The mid-oesophagus includes that portion of the oesophagus that has been effected by torsion. The posterior oesophagus extends into the stomach.

The evolution of the oesophageal glands has been investigated by a number of workers (Amaudrut 1898; Fretter & Graham 1962; Ponder 1970a, 1973a; Salvini-Plawen & Haszprunar 1987; Salvini-Plawen 1988) and is now reasonably well understood. The primitive state seen in the outgroups and in Patellogastropoda (Bush 1989) is to have large oesophageal pouches. The mid-oesophagus of patellogastropods resembles that of neritopsines, although in the latter the oesophageal glands are separated into two large pouches (Fretter 1965) with a different histology (Fretter 1984a), which Whitaker (1951) regarded as a combination of buccal pouches and oesophageal glands. In vetigastropods, the lining of the oesophageal glands forms distinct papillae (Salvini-Plawen & Haszprunar 1987), although how universal this character is in that group is unclear. Changes to the mid-oesophageal region in caenogastropods are considerable, as discussed briefly below.

The primitive ventral folds in the oesophagus are lost in most caenogastropods, although they are present in architaenioglossans such as *Marisa* (Lutfy & Demian 1967) and Cyclophoridae (Schneider 1920), with a rudiment in the primitive neotaenioglossan genus *Provanna* (Warén & Ponder 1991). The separation of the dorsal folds from the oesophagus and their involvement in the gland of Leiblein, which is also derived from the oesophageal gland, occurs to a varying degree in neogastropods (Ponder 1973a). The evolution and homology of the gland of Leiblein and the toxoglossan poison gland have been discussed by Ponder (1970a, 1973a) and Fretter & Graham (1994). The poison gland is assumed to have evolved from a gland of Leiblein-like state (Ponder 1970a).

Loss of the oesophageal gland has occurred in many caenogastropods and is often correlated with the presence of a crystalline style (Graham 1939). There are, however, many taxa that lack both crystalline style and oesophageal glands and a few in which they are present together (for example, some cerithioideans, Houbrick 1988).

The Stomach

There is a considerable literature on stomach morphology (for example, Graham 1932, 1949; Fretter & Graham 1962; Smith, E.H. 1967b). Simplification of the stomach has occurred in some groups, particularly Neogastropoda (Smith, E.H. 1967b). It is thought that the primitive gastropod stomach had a style sac with a protostyle (a rod of mucus-bound food) (J.E. Morton 1953a; Salvini-Plawen 1988) and a chitinous gastric shield. A crystalline style occurs, probably convergently, in several caenogastropod groups.

The patellogastropod stomach is small and simple (Graham 1932). In most other herbivorous or deposit-feeding gastropods the stomach is generally similar to that of the genus *Calliostoma* described above (Fig. 15.11), although only vetigastropods have a spiral caecum, and others have a short, simple caecum, or, sometimes, none (see Fig. 14.25C). Graham (1949, 1985) suggested that a spiral caecum is a primitive feature of the gastropod stomach, but this structure is now thought to be a synapomorphy uniting the Pleurotomarioidea and Trochoidea (Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a). There is a small ciliated 'sorting' caecum in many caenogastropods (Graham 1949; Smith, E.H. 1967b). Although absent in most neogastropod stomachs, a gastric shield and caecum are present in many buccinids and related taxa (Smith, E.H. 1967c).

Some caenogastropods, such as stromboideans, rissooideans and many cerithioideans, have a crystalline style in the style sac (Graham 1939; Fretter & Graham 1962).

The Intestine

Typically, reduction in length of the intestine has been associated with the change from herbivory to carnivory, and a diminished need to consolidate faecal matter (Fretter & Graham 1962; Owen 1966). However, simplification of intestinal looping patterns is a predominant trend within the Gastropoda and is not necessarily associated with feeding. The intestine of patellogastropods and vetigastropods is coiled. In more highly derived patellogastropods there is a marked reduction in intestinal length (Lindberg 1988a, 1988b), and yet most patellogastropods have similar diets. Thus, in this case at least, there is no apparent relationship between food type and intestinal length; shortening is probably a consequence of paedomorphosis (Lindberg 1988b). Among caenogastropods which employ a wide range of feeding strategies similar intestinal configurations are seen. In most lower caenogastropods, including neotaenioglossans, the first intestinal loop is arched backwards and pressed around the style sac, a condition not seen in other gastropods. In neritopsines and vetigastropods, the rectum passes through the heart. In patellogastropods (Lindberg 1988a) and caenogastropods, the rectum does not pass through the heart.

Various adaptations enable faecal material to be transported from the mantle cavity. These include a slit or aperture in the shell with the anus remaining in the plesiomorphic posterior position and the extension of the rectum along the right side of the mantle cavity so that the anus is located near the edge of the shell. The anterior migration of the anus has apparently occurred independently in the Trochoidea, Neritopsina and Caenogastropoda (Ponder & Lindberg 1997). Gastropod faecal material has been studied in detail by Arakawa (1963, 1965, 1968, 1972). Primitive gastropods produce a faecal string, whereas caenogastropods and neritopsines produce pellets.

Carnivory

Few vetigastropods graze on sessile animals (for example, species of *Calliostoma*, Perron 1975; Perron & Turner 1978), and those that do show few modifications for carnivory. Among caenogastropods there are many carnivorous groups, some of which show considerable modifications. Since they are relatively slow moving, their prey is usually limited to sessile animals like sponges, barnacles, ascidians, or to animals that typically become immobile when disturbed, such as bivalves or other gastropods. The carnivorous habit probably arose out of general browsing, which presumably results in the incidental inclusion of animals in the food. Several gastropod groups have undergone major radiations following the adoption of a carnivorous diet. These include the Neogastropoda (Ponder 1973a; Taylor, J.D., Morris & Taylor 1980; Taylor, J.D. & Morris 1988), and several groups within the caenogastropod Neotaenioglossa, especially the (probably paraphyletic) Ptenoglossa, the Tonnoidea and the Naticoidea. Some neogastropods can capture relatively active prey and some cones even prey on fishes. One group of caenogastropods, the Carinariidea (heteropods), have become active, swimming predators.

15. PROSOBRANCHS

In most carnivores a proboscis (introvert) has developed, enabling attacks on different parts of the prey body, or on prey hidden in crevices or burrows. For example, on protrusion, the proboscis can enter the ostia of sponges (*Cerithiopsis*, *Triphora*; Fretter 1951b) or tunicates (*Simnia*, Fretter 1951a; *Trivia*, Fretter 1951a; *Velutina*, Diehl 1956) and so reach parts more nutritious than the outer layers. Several types of proboscis have evolved in neogastropods enabling them to attack a wide range of prey. Various more elaborate methods of attack allow utilisation of a broader range of prey. The development of large and powerful jaws against which the radular teeth may operate permits biting, as in *Janthina* (Graham 1965a) and *Epitonium* (Perron 1978), which bite pieces from the cnidarians on which they feed. The ptenoglossate radulae of these snails, composed of many rows of numerous fang-like, recurved teeth, aid ingestion of fragments bitten from the prey.

A further device assisting attacks by carnivorous caenogastropods on shelled prey is the ability to bore (see review by Kabat 1990a), found in some tonnoideans, naticoideans (Ziegelmeier 1954) and muricids. Boring has also been recorded recently in some marginellids (Ponder & Taylor 1992) and the buccinid genus *Cominella* (Peterson & Black 1995). The mechanism in muricids was detailed by Carriker (1981) in his summary of classic work on the oyster drill, *Urosalpinx cinerea*. In naticoideans, boring involves the activity of the accessory boring organ located on the ventral tip of the proboscis (Fig. 15.13), and in muricids it involves a similar structure in a pit on the sole of the foot. Boring is achieved by alternating periods of radular rasping and applications of this accessory boring organ to the borehole. The secretions of the latter include hydrochloric acid, carbonic anhydrase, and chelating agents which attack the calcareous shelly matter after it has been exposed by the action of a proteinase which attacks the conchiolin matrix of the shell. The radula, which is not hard enough to rasp untreated shell, therefore removes softened shell. The shell fragments are swallowed flake by flake until a hole is made allowing the proboscis to enter and rasp the flesh. Naticoideans bore bivalves exclusively, dragging them under sand whereas muricids are more generalist feeders, attacking bivalves, barnacles or other gastropods, depending on size and the availability of the prey.

An acid secretion, sometimes including a toxic substance, is also used by tonnoideans to kill their echinoderm prey and to penetrate their calcareous testes (Weber 1927; Day 1969; Hughes, R.N. & Hughes 1981). Sulphuric acid is produced in glands associated with, and perhaps specialised parts of, the salivary glands. The role of the radula in the process of boring is limited to the removal of calcium sulphate produced by the acid. The secretion is more strongly acid (pH 1–0.3) than that of the North Atlantic muricid *Urosalpinx* (pH 4.1–3.8), and greater in volume. As the echinoderm test is less dense than a bivalve shell, tonnoidean boring rates (0.1 mm.min^{-1}) are much faster than those of muricids ($0.3\text{--}0.5 \text{ mm.day}^{-1}$) (see reviews by Kabat 1990a; Fretter & Graham 1994). Houbbrick & Fretter (1969) described the use of an acid saliva in other tonnoideans (*Cymatium* and *Bursa*) as a toxin to inactivate the gastropod prey and permit the proboscis to enter the mantle cavity.

Though unable to bore, some neogastropods, such as species of the Northern Hemisphere whelk genus *Buccinum*, are still able to open bivalve shells, largely by sudden thrusts of the edge of their own shell between the valves of the prey to wedge it open or even cut the adductor muscle (Nielsen 1975). The extent of opening need only be quite small, as Nielsen (1975) showed that the proboscis of a whelk could pass through a gap of only 1.3 mm. The American muricid *Acanthina spirata* uses a prominent spine on the outer lip of the shell to perforate the shells of barnacles (Perry 1985). Perry found that when forced to drill by experimental removal of the spine, the muricid's feeding time was increased by 75–500%.

The diets of Northern Hemisphere buccinids (such as species of *Buccinum* and *Neptunea*) comprise mainly small annelid worms (Pearce & Thorson 1967; Taylor, J.D. 1978a), and the same is probably true of at least most buccinids and the smaller turrids (Pearce 1966).

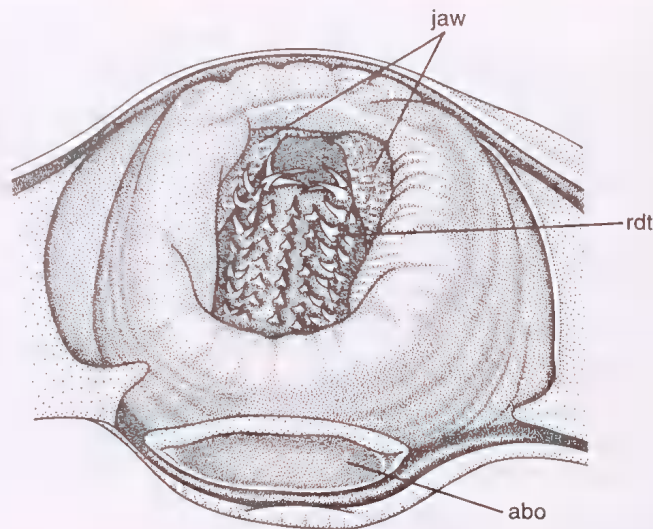


Figure 15.13 The tip of the proboscis of *Naticarius millepunctatus* (Caenogastropoda, Naticidae), showing the accessory boring organ on its ventral side. The mouth is open, displaying the tip and underside of the odontophore with the radular teeth folding away at the former, opened out at the latter. Latero-dorsally within the buccal cavity a jaw is visible. abo, accessory boring organ; jaw, jaws; rdt, radular teeth. (After Hyman 1967) [B. Scott]

The larger toxoglossans (Conoidea), such as the Conidae, have evolved a feeding mechanism which enables them to capture rapidly moving, free-swimming, prey such as fishes. Their adaptations involve changes in radula, proboscis, and glandular equipment. The last includes a poison gland, derived in part from the oesophageal glands, which secretes a neurotoxin and discharges to the buccal cavity. Radular evolution in turrids and cones has been discussed by Shimek & Kohn (1981) and Taylor, J.D. *et al.* (1993). 'Primitive' taxa have five teeth in each transverse radular row, all fastened to the radular membrane, and together forming a powerful cutting tool. In some, the central tooth of each row is lost (some Clavinae), followed by the lateral teeth, leaving only marginals which are produced alternately right and left and may become detached from the radular membrane so as to lie singly and freely in the buccal cavity. Alteration in the shape of the teeth accompanies these changes such that they become rolled into scrolls, their edges barbed, and the central hollow filled with the secretion of the poison gland. In the more modified toxoglossans another change has occurred. The proboscis has become an apparatus for moving a tooth forward to the mouth where it is gripped with the lips. In this position it is used to stab and immobilise prey (worms, other molluscs, fishes) which are then ingested whole.

The pelagic carinarioidaeans (heteropods) are carnivores. They swim upside down and locate their prey by sight, constrained by their own low speed to capturing slow swimmers such as jelly-fish, salps and worms (Thiriou-Quévieux 1973).

Typically the carnivore stomach is simple. However, the oesophagus of many neogastropods has become more complex, possibly coupled to the development of the proboscis. The glandular part of the food channel no longer occurs; there is a separate gland, the gland of Leiblein. This gland is connected to the oesophagus by a narrow duct, the line of separation marked by a histologically distinct band of cells. In many taxa the dorsal folds of the oesophagus have also become glandular and are incorporated in the duct and, in some, form part of the gland (Ponder 1973a). Anteriorly, a swollen valve of Leiblein marks the anterior limit of the mid-oesophagus. This presumably prevents forward movement of the gut contents as the proboscis is protruded (Amaudrut 1898; Graham 1941; Ponder 1973a).

Suspension-feeding

The respiratory stream entering the mantle cavity of aquatic species inevitably contains some suspended matter. In species with a single gill, the cilia on the pallial floor sweep large particles off to the left, and small ones join the exhalant current on the right. Some of the finest particles may reach the ctenidium, be strained out of the current, coagulated in mucus and added to the exhalant stream. Some gastropods have become partly or wholly dependent on fine organic particles for food. The habit has evolved independently on a number of separate occasions and is seen in the trochoideans *Umbonium* (Fretter 1975) and *Bankivia* (Hickman & McLean 1990), the deep-sea hot-vent *Neomphalus* (Fretter *et al.* 1981), the Viviparidae (Cook 1949), and the neotaenioglossans *Bithynia* (Schäfer 1952, 1953; Lilly 1953), Turritellidae (Graham 1938; Hickman 1985; Hughes, R.N. 1985a), Capulidae (Yonge 1938), Calyptraeidae (Orton 1912; Werner 1953) and Vermetidae (Yonge 1932; J.E. Morton 1951b, 1951c, 1951d; Hughes, R.N. 1985b). Filter-feeding is commonly associated with a sedentary life style or, as in vermetids, a totally immobile one. The mechanism is essentially identical in all, and is elaborated only in details (Werner 1952, 1959).

The Calyptraeidea is one of the groups most modified for suspension-feeding. In the calyptraeid genus *Crepidula*, a mucous net produced on the inner surface of the inner mantle edge is stretched across the left entrance to the mantle cavity (Fig. 15.14). This traps the largest particles as they enter, and they are transported by cilia to a pouch in the mantle skirt over the head, from whence they are periodically withdrawn by the radula. Fine particles pass this filter, but are caught on a sheet of mucus lying over the lower surface of the gill (Fig. 15.9). This is produced from the glandular endostyle on the ctenidial axis and moved steadily over the gill surface to the free edge, where it meets a similar sheet travelling along the upper gill surface. At the tip the two sheets, with their entrapped particles, are rolled into a cord and deposited in a food groove (Fig. 15.9) on the floor of the mantle cavity (the dorsal surface of the head), from there they are driven by cilia to where they can be reached by the radula. The trap for food in *Crepidula* is thus a branchial mucous sheet, as in protochordates, and the mechanism is therefore different from that in bivalves where elaborate latero-frontal cirri form the trap (Owen 1974).

The success of such a ciliary-mucous mechanism depends on several factors, among them the areas of the filter and the lateral cilia on the gill, producing the force driving the current. Both can be increased by elongation of the gill thus providing space for more lamellae, and by narrowing the lamellae to form longer filaments, so increasing the ciliary surface. Such changes are obvious in *Umbonium*, *Neomphalus*, calyptraeids and turritellids. They are much less marked in viviparids, bithyniids and capulids, which appear to use ciliary food-collecting to supplement what they obtain by other means. The same is true of the changes visible in radular teeth (Hickman 1984c) since their manipulation of a mucous string calls for less strength than does rasping. The teeth are little changed in those taxa which still rasp, whereas in species relying solely on ciliary-feeding the teeth are often reduced to scale-like structures nearly devoid of cusps. In most suspension-feeders the salivary glands are reduced and the oesophageal glands are vestigial. Other changes in the gut include the marked reduction of the gastric caecum, though most other stomach features are retained. The style sac, which typically acts as an organ compacting faecal matter, produces a crystalline style in caenogastropod suspension-feeders paralleling that of bivalves.

Parasites

The radula is reduced or lost in parasitic taxa. Some parasitic snails, such as those belonging to the eulimid genus *Pelseneeria*, live among spines and pedicellariae on the test of various echinoids, browsing on the epidermis (Ankel 1936b). Many eulimids may feed in a similar way, though with the development of a proboscis they can penetrate the body of the echinoderms with which they associate and take up fluids or tissues. Some have only a slight and probably temporary association with a host

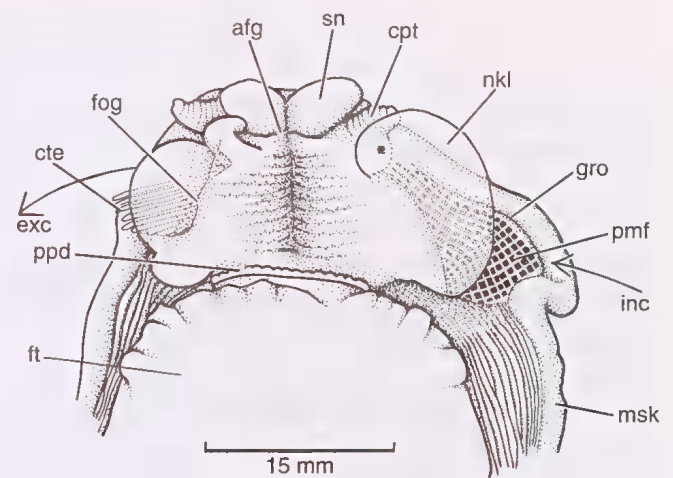


Figure 15.14 The anterior half of body of *Crepidula fornicata* (Caenogastropoda, Calyptraeidae), ventral view. Arrows show direction of water current. afg, anterior end of food groove; cpt, cephalic tentacle; cte, ctenidium, partly seen by transparency; exc, exhalant current; fog, food groove seen by transparency; ft, foot; gro, groove along which food and mucus from pallial filter travel to food pouch; inc, inhalant current; msk, mantle skirt; nkl, neck lobe; pmf, pallial mucous filter; ppd, propodium; sn, snout. (After Fretter & Graham 1962) [B. Scott]

(Warén 1983a), but others (for example, *Stilifer*, *Echineulima*) become immobilised, with the proboscis permanently embedded in the host tissue (Rosen 1910; Lützen 1972; Lützen & Nielsen 1975). In some species that have become internal parasites, some of the characteristic molluscan features are eventually lost. Reduction reaches an extreme in the few species (for example, *Entoconcha* species) which are parasitic in the gut of holothurians (Lützen 1979). In these molluscs, the males have become dwarfed and live embedded in the body of the female; the female itself is represented almost entirely by a gonad.

Some *Capulus* species live on bivalve shells, or on ciliary-feeding gastropods, and extract food or pseudofaeces from the mantle cavity of the host (Sharman 1956; Thorson 1965). Other species of *Capulus* live on pectinids and etch a hole through the shell to reach the pseudofaeces (Orr 1962).

The Circulatory System and Respiration

The general features of the gastropod circulatory system are described in Chapter 14. Here we describe the 'prosobranch' system in more detail, including, as for other systems, a description of *Calliostoma*.

The heart typically consists of a ventricle and one or two auricles within the pericardial sac. A non-contractile aortic bulb is also sometimes present (Hyman 1967). In some gastropod groups the ventricle is penetrated by the rectum, the result of the ventricle enveloping the rectum in ontogeny, but this is not the case in patellogastropods and caenogastropods. The number of auricles is usually correlated with the number of gills, although Trochoidea and many neritopsines have two auricles and one gill. Whereas the deep-sea hot-vent *Neomphalus* has one auricle and the ventricle is penetrated by the rectum (Fretter *et al.* 1981), the primitive conditions of the heart are generally retained in Neritopsina and Vetigastropoda. In all apogastropods (caenogastropods and heterobranchs) the rectum does not enter the pericardium and there is a single auricle.

Virtually all 'prosobranchs' have the same basic circulation pattern (Fig. 15.15; Fretter & Graham 1962; Ponder & Lindberg 1997). Blood passes from the kidney(s) to the mantle and gills and then to the auricle(s). In some (patellogastropods, dibranchiate vetigastropods), this is modified with blood from the kidney(s) passing separately to the mantle and the gill(s) and then from both

15. PROSOBRANCHS

to the auricle(s) (Fig. 15.15A). In trochoideans (Fig. 15.15B) and caenogastropods (Fig. 15.15C), blood circulates from the kidney to the mantle and the gill (pallial vessels connect to the afferent branchial vessel along its length). In heterobranchs the basic pattern is different, with blood passing from the mantle to the (pallial) kidney to the auricle.

The Circulatory System of *Calliostoma*

In trochoideans such as *Calliostoma zizyphinum*, the anterior wall of the pericardial cavity is in contact with the innermost end of the mantle cavity (Fig. 15.8). The heart consists of a ventricle, through the centre of which runs the rectum, bordered anteriorly by a left auricle and posteriorly by a right auricle. The pericardial cavity communicates with each of the two kidneys by a renopericardial canal. A vessel arises from the left wall of the ventricle and divides to form an anterior and a posterior aorta, emerging from the anterior and posterior walls of the pericardium, respectively.

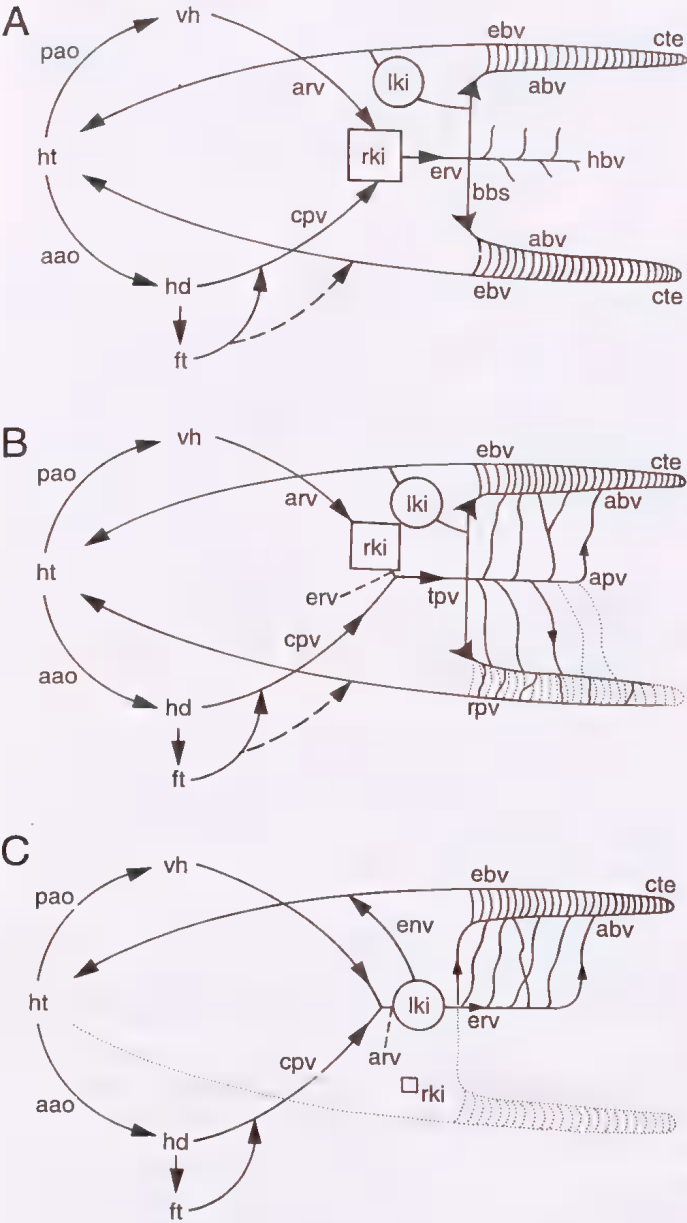


Figure 15.15 Prosobranch vascular systems, represented diagrammatically. A, *Haliotis* (Vetigastropoda, Haliotidae). B, a trochid (Vetigastropoda). C, Caenogastropoda. Solid lines indicate vessels occurring; dashed lines mark vessels which probably exist; dotted lines are vessels which have been lost. aao, anterior aorta; abv, afferent branchial vessel; apv, anterior pallial vein; arv, afferent renal vessel; bbs, basibranchial sinus; cpv, cephalopodal vein; cte, ctenidium; ebv, efferent branchial vessel; env, efferent vessel of nephridial gland; erv, efferent renal vein; ft, foot; hbv, hypobranchial vessels; hd, head; ht, heart; lki, left kidney; pao, posterior aorta; rki, right kidney; rpv, right pallial vein; tpv, transverse pallial vein; vh, visceral hump. (After Fretter & Graham 1962) [I. Hallam]

A schematic plan of the trochoidean circulatory system is shown in Figure 15.15B. The posterior aorta passes up the visceral mass and branches, giving rise to vessels to the part of the right kidney posterior to the heart. This aorta then enters the deeper parts of the visceral mass and passes to the columellar side, running up the visceral coil in this position to the summit of the coil. The posterior aorta supplies arteries to the stomach, digestive gland and gonad. Blood from all these vessels enters a large visceral haemocoel surrounding these organs. The anterior aorta passes forwards on the left side of the body at the level of attachment of the mantle skirt and ventral to the efferent branchial vessel. It comes to lie alongside the anterior loop of the intestine, at the anterior end of which it penetrates the transverse septum, the posterior limit of the haemocoelic spaces in the head.

The anterior aorta then crosses to the right side, adherent to the septum, and passes forwards towards the posterior limit of the buccal mass. There it gives rise to an anterior and two lateral pedal arteries, the latter passing back along each side of the foot. The anterior aorta continues forward in the floor of the cephalic haemocoel to a point midway along the length of the odontophoral cartilages. There it divides into the buccal artery, which passes dorsally and opens to sinuses in the odontophore and around the radular sac, and two lateral cerebral arteries which pass forward to the cerebral ganglia and also branch to the snout, the eye stalks and the tentacles.

All blood from the head-foot flows into a cephalopodal vein which passes posteriorly and then dorsally towards the mantle skirt. As it does so, it is joined by the efferent vein from the right kidney. At their junction arises the transverse pallial vein, which supplies blood to the mantle skirt, and where the three veins meet a valve controls the blood flow. Since the right kidney receives all blood from the visceral haemocoel, this valve controls all blood distributed by the aortae and returning to the heart. The transverse pallial vein (Figs 15.8, 15.15B) crosses the mantle skirt from right to left ventral to the rectum, and along its course gives off a relatively small vessel to the left kidney (from where the blood ultimately flows to the left auricle) and then supplies two much larger vessels. One of these larger vessels, the afferent pallial vein, runs forward, parallel with the rectum, vascularises the left and right hypobranchial glands and sends a branch to the afferent branchial vessel (Figs 15.8, 15.15B) near the free tip of the ctenidium before approaching the mantle edge as the anterior pallial vein (Fig. 15.8). The other vessel, the afferent branchial vessel (Figs 15.8, 15.15B), receives the transverse pallial vein about half way up the length of the ctenidium. Along this final part of its course the transverse pallial vein vascularises the left hypobranchial gland (Fig. 15.8). Blood flowing across the mantle skirt to the right enters the efferent pallial vein (Fig. 15.8) which passes back to the smaller right auricle.

The diagrams in Figure 15.15 enable comparison of the circulatory systems of a dibranchiate vetigastropod, a trochoidean (like *Calliostoma zizyphinum*) and a typical caenogastropod. The major differences are the reduction and loss of the circulatory system associated with the right ctenidium. This is retained in part in trochoideans (even though the right gill is absent, its original position is indicated in the diagram) in the form of the efferent (or right) pallial vein, but is completely lost in caenogastropods. In addition, in caenogastropods the blood flow is switched to the left kidney (Fig. 15.15C), compared with primarily the right kidney in vetigastropods and patellogastropods. Patellogastropods differ from vetigastropods in having two main routes by which the blood from the right kidney may reach the auricle, via the mantle edge (and the secondary gills when present) and via the ctenidium, when it is present.

Respiration

Oxygen is transported in the blood by the respiratory pigment haemocyanin in most gastropods, but haemocyanin is absent from species small enough to allow adequate passive gas exchange (Fretter & Graham 1962). In the typical marine 'prosobranch', respiratory gas exchange occurs mainly across the surfaces of the

ctenidial leaflets, and involves a counter-current exchange system. Because the mantle skirt is also richly vascular and exposed to the same water current, exchange of gases must also occur there and to a lesser degree over parts of the head-foot.

The rates of respiration and of metabolism may be related to a variety of factors such as temperature, size of animal, and nutritional state. Newell and co-workers (Newell & Northcroft 1967; Newell & Pye 1970a, 1970b, 1971) have categorised these into an active fraction and a quiescent fraction. Bayne & Scullard (1978) reported that oxygen consumption in the intertidal European muricid, *Nucella lapillus*, rose in summer and fell in winter. This was partly due directly to temperature and partly to the effect of feeding for, like many other gastropods, *N. lapillus* stops feeding when the temperature falls below 8–10°C.

Respiratory activity in intertidal species depends on the length of the period of exposure to air and such environmental variables as humidity. Some increased vascularisation of the mantle skirt permitting greater respiratory exchange during exposure to air has been reported by Deshpande (1957) in upper shore versus lower shore trochids. Similar variation in tolerance of water loss has been shown in patellid species. The European limpet *Patella vulgata* from high levels can survive 60% water loss, and those from low levels 50% water loss, whereas *P. aspera*, living in wet situations at low water mark in the same region, can withstand only 30% water loss (Davies 1969). Survival depends in part upon the ability of the animal to retain water in the mantle cavity, and upon a good fit of the shell margin to the substratum in limpets, or between the operculum and shell in snails. However, working with European gastropods, Houlihan, Innes & Dey (1981) found little correlation between the amount of fluid in the mantle cavity and level on the shore, suggesting that the high shells of upper shore patellids may not serve to store greater volumes as proposed by Orton (1929). They did find a correlation between the level on the shore and respiratory activity in air in *Gibbula cineraria*, *Littorina littorea* and *Nucella lapillus*. Lowell (1984), however, found that shell shape and volume in *Collisella pelta* (Lottiidae) are significant factors in allowing respiration to continue in air. Even when aerobic respiration is inhibited by excessive water loss snails may survive long periods without direct access to oxygen (Patanè 1946a, 1946b, 1955), presumably then dependent on anaerobic metabolism.

Changes in the above patterns necessarily occur in freshwater and terrestrial taxa, the former needing to retain salts and lose water, the latter to retain both, and in addition, to acquire a different respiratory mechanism.

Terrestrial species lose the ctenidium and osphradium though a vestige of one or other may remain. In their absence, the mantle skirt, richly vascularised even in aquatic species, becomes the main site of gaseous exchange. In the amphibious architaenioglossan family, Ampullariidae (Bouvier 1888; Prasad 1932; Andrews, E.B. 1965), the left side of the mantle skirt is expanded, pushing the ctenidium to the right, and the two parts of the mantle cavity are separated functionally by a fold rising from the pallial floor. The left half acts as a lung, ventilated by in-and-out movements of the head (Kasinathan 1975). This part is used when the animal breaks the surface of the water in which it lives, in some species by way of a tubular siphon extending from the mantle edge. The gill in the right half is still used when the water is well oxygenated. The opening of the mantle (pulmonary) cavity remains wide in many amphibious and terrestrial caenogastropods, such as cyclophorids, but becomes small and slit-like in some ampullariids (Hägler 1923). Aerial respiration becomes difficult, though oxygen requirements fall, during the periods of aestivation which dry seasons often force upon terrestrial snails. Respiration appears to be facilitated by a number of devices in cyclophorids (Rees 1964), including apertural notches or tubular outgrowths (see Fig. 14.18) which allow air to pass behind the operculum of the retracted snail, probably pumped by the slight movements of the animal which, as in the pulmonate genus *Helix*, continue even during aestivation (Fischer 1931).

Excretion, Osmoregulation

The Renal System and Excretion

The by-products of metabolism are conveyed by the blood to the excretory organs (kidneys, renal organs). The right and left kidneys of vetigastropods, unlike the paired kidneys of other molluscan classes, have long been known to differ in structure and function (Perrier 1889; Cuénot 1899; Harrison 1962; Delhaye 1976). E.B. Andrews (1988) gave a detailed description of the function, structure and evolution of gastropod kidneys. The post-torsional left kidney is present in all gastropods, and the right kidney is maintained in many of the basal groups (Fig. 15.16). In those groups with both kidneys (including the Patellogastropoda; Fig. 15.16A–D) the post-torsional right kidney is concerned with nitrogen excretion, the left with the ionic composition of the blood (Delhaye 1976; Andrews, E.B. 1988). The post-torsional right kidney has apparently been lost in several groups independently, becoming incorporated in the genital duct (Fig. 15.16E, F). In these groups the left kidney takes on the functions of both left and right kidneys (Andrews, E.B. 1985, 1988). Fissurellids (Fig. 15.16C) and patellogastropods (Fig. 15.16B) appear to have acquired a small left kidney independently (Andrews, E.B. 1988). In vetigastropods, the right kidney is at least partly embedded in the visceral mass and the left lies wholly within the mantle skirt. The separation of functions probably occurs because the right kidney receives largely deoxygenated blood, rich in waste products from the viscera, whereas the left receives blood from which the waste has been removed and oxygen taken up on passage through the ctenidium (Andrews, E.B. 1985).

The Excretory System of *Calliostoma*

As in other vetigastropods, the two kidneys in the genus *Calliostoma* are dissimilar in size and function (Figs 15.8, 15.16D). The left is compact and lies totally within the mantle skirt, isolated from the viscera (Fig. 15.8). Its primary function is the resorption of organic and ionic solutes from the blood. The right kidney – conspicuous in some species owing to its rose-pink colour – is large and more diffuse, and spreads through the visceral haemocoel. A dorsal lobe, between the posterior wall of the pericardium and the digestive gland, spreads anteriorly under the heart and through the haemocoel associated with the right limb of the anterior intestinal loop. At the base of this anterior extension, close to the pericardium, a tube-like section passes into the mantle skirt to the right of the rectum and leads to the external opening. The right kidney is responsible for nitrogen excretion, but it also has a reproductive role; the gonadal duct enters near the opening of the renopericardial canal in both sexes. From this point a ciliated tract leads to the external urinogenital opening. In males, the right and left kidney apertures lie level with one another, but in females the right one is placed considerably further forwards since a glandular section is added which lies in the thickness of the mantle skirt and is related to the production of a spawn mass.

The left kidney has a solid construction and is referred to as the papillary sac because it contains stout internal papillae. The walls are more muscular than those of the right kidney and are highly vascular, the vascularisation being most marked in the area of the nephridial gland where papillae are shorter and fewer. The L-shaped nephridial gland is involved in the transport of ions and small molecules. It extends along the posterior pericardial wall and anteriorly alongside one of two main longitudinal vessels visible on the surface of the papillary sac. This nephridial gland vessel connects with the efferent branchial vessel at the mouth of the left auricle. At this point, a transverse vessel running in the pericardial wall opens. This transverse vessel is a continuation of the second longitudinal vessel originating anteriorly from the transverse pallial vein and receives a number of vascular inlets from the kidney. Blood in these vessels must come under the direct influence of the heart beat. The anatomical arrangement (Andrews, E.B. 1985) strongly suggests that oxygenated blood flows into the nephridial gland vein from the efferent branchial vessel at auricular systole and back to the auricle at diastole. Some

15. PROSOBRANCHS

of this blood must circulate through the kidney and return to the auricle via its connections with the transverse vessel. Urine produced by the left kidney would thus be a filtrate of oxygenated blood already depleted of nitrogenous excretory products (purines and ammonia) by the right kidney, and with a high pH.

The epithelial cells of both kidneys show features characteristic of active transport. The apical surfaces bear cilia and microvilli, the cytoplasm contains coated pits and vesicles apically, and basally the surface area in contact with the blood is increased by extensive folding. The epithelium of the papillary sac has two types of cell involved in active transport. One is confined to the nephridial gland, the other is cuboidal, with long basal extensions into the blood space penetrating the papillae. The apical cytoplasm of these cells shows great activity suggestive of selective uptake of solutes from the primary urine, which is a filtrate of post-branchial blood. Transport across the kidney epithelium may also occur in the opposite direction, from blood to lumen, as demonstrated by Delhaye (1976) in *Monodonta*. In the nephridial gland, the cell bodies are invaginated by a network of blood channels and the in-foldings of their basal membrane are associated with mitochondria, indicative of an involvement with ion transport.

Material of larger molecular weight is extracted from the blood by the pinocytic activity of the epithelial cells, and particulate matter is taken up by phagocytosis in numerous amoebocytes in the blood spaces.

The right kidney is well placed to undertake nitrogenous excretion as the blood it receives is almost at the end of its course round the body. This prebranchial blood – that is, prior to oxygenation in the gill – is laden with the products of metabolism, has low oxygen and high carbon dioxide tensions and the pH is perhaps the lowest in the body. The wall of the right kidney is a spongy mass of tubular evaginations of epithelium, except in the extension leading to the external opening. Here the excretory cells are multivacuolate with layered excretory spherules. The afferent renal vessel enters the posterior lobe and branches over the wall and, although prebranchial blood bathes the cell bases, primary urine covers their inner (luminal) surface. Consequently, differences in pH and solute concentration may create conditions under which ammonia diffuses into the lumen and is trapped in the urine. The ammonia would inhibit the sodium transport system used in the resorption mechanism, but would not prevent uptake from the primary urine by pinocytosis. The major site of excretory activity is where the kidney abuts the digestive gland. The vacuoles of the renal cells have a core of lipofuscin (Delhaye 1976), which suggests that lysosomes are involved in the early stages of formation of the excretory spherules, providing an area on which other materials precipitate. Within the elaborate vacuolar system, nitrogenous waste, lipofuscins, melanins, and ferric iron are the most important constituents of the excretory granules. The large vacuoles containing the granules are ultimately shed as blebs of cytoplasm nipped off from the cell membrane, and the primary urine now plays a second role – as a vehicle for their transport to the exterior.

Evolution of the Kidneys

The left kidney of most vetigastropods, as in the genus *Calliostoma*, is modified to form a 'papillary sac' (Fleure 1902; Fretter & Graham 1962; Andrews, E.B. 1988), even in fissurellids where it is much reduced (Fig. 15.16C; Andrews, E.B. 1988).

The position of the adult kidneys relative to the pericardium varies between groups (Ponder & Lindberg 1997). Most vetigastropods have kidneys on each side of the pericardium and rectum, which is the plesiomorphic state for Gastropoda (Figs 15.8, 15.16A, C, D). However, in some 'archaeogastropods', such as *Neritopsina* (Fig. 15.16E) and *Neomphalidae* and in all apogastropods – caenogastropods (Fig. 15.16F) and heterobranchs – only the post-torsional left kidney remains as a functional kidney. It lies to the right of the pericardium on the left side of the rectum, presumably as a result of torsion. This loss of a functional right kidney has occurred independently in several gastropod lineages, the anatomical and physiological consequences being met in different ways (Andrews, E.B. 1981, 1988). Most 'monotocardian' groups have a nephridial gland associated with the left kidney, but some caudoconchids (Haszprunar 1987a) and neritopsines (Fig. 15.16E; Andrews, E.B. 1988) do not. Some groups with two kidneys such as trochoideans (Fig. 15.16D), *Neomphalus* (Fretter *et al.* 1981) and *Peltoispiridae* (Fretter 1989) also have a nephridial gland associated with the left kidney. Cyclophoroideans, all of which are terrestrial, have a pallial kidney which is a 'kidney of accumulation' (Andrews, E.B. 1988). The kidney of the freshwater Ampullariidae is highly modified and lacks a nephridial gland (Andrews, E.B. 1988), although one is present in *Viviparus*. The kidney of these animals is partly in the pallial roof, whereas in other caenogastropods (with the exception of some cerithioideans) typically it is entirely or primarily visceral, a condition unlike the primarily pallial position of the left kidney in vetigastropods and heterobranchs.

The loss of a functional right kidney in ancestral caenogastropods required the left kidney to deal with nitrogenous excretion along with its other functions. It lies at least partly in the viscera so that the left wall of the kidney, which bears the nephridial gland – responsible for ionic control and resorption of solutes – has

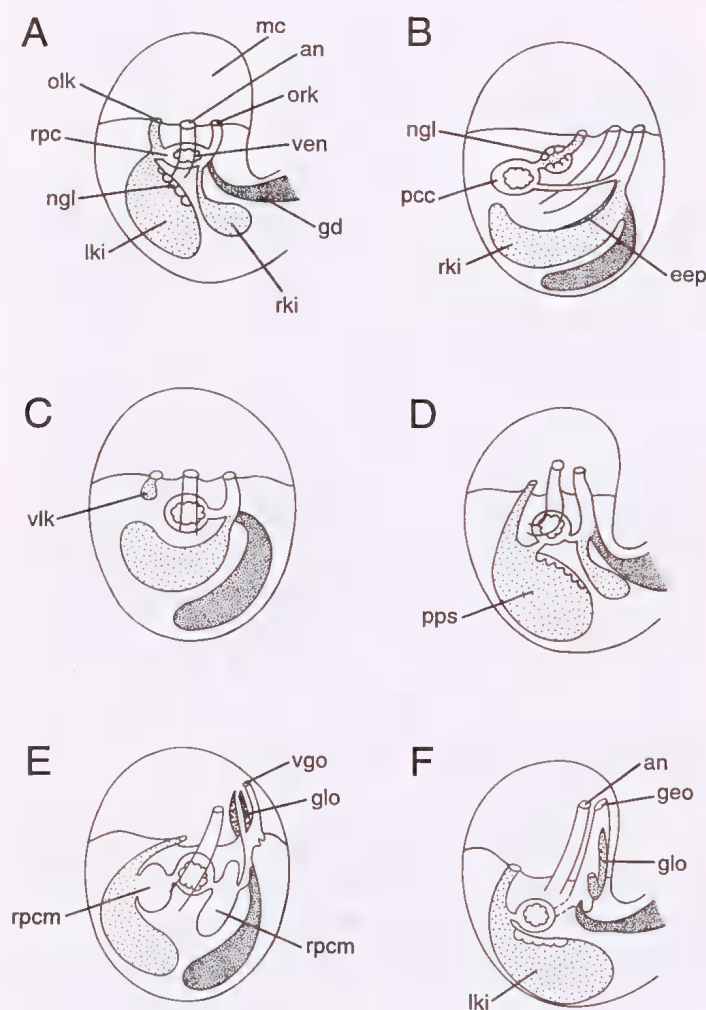


Figure 15.16 Prosobranch excretory systems. A series of diotocardian and a littoral monotocardian systems, represented diagrammatically. A, pleurotormioidean (Vetigastropoda). B, patelloidean (Patellogastropoda). C, *Diodora* (Vetigastropoda, Fissurellidae). D, trochid (Vetigastropoda). E, *Theodoxus* (Neritopsina, Neritidae), female. F, Caenogastropoda, female. an, anus; eep, excretory epithelium; gd, gonad; geo, genital opening; glo, glandular oviduct; lki, left kidney; mc, mantle cavity; ngl, nephridial gland; olk, opening of left kidney; ork, opening of right kidney; pcc, pericardial cavity; pps, papillary sac; rki, right kidney; rpc, renopericardial canal; rpcm, modified renopericardial canal; ven, ventricle; vgo, opening of vagina; vlk, vestigial left kidney. (Modified after Andrews, E.B. 1981)

[I. Hallam]

retained its connection with the efferent branchial vessel and is supplied with oxygenated blood. The right dorsal wall of the kidney, which receives nearly all the blood from the head-foot and visceral mass on its way to the ctenidium, extracts nitrogenous waste and discharges it to the lumen. Its surface is modified and folded to provide sufficient area for this to be done effectively. Though performing essentially the same role as the patellogastropod or vetigastropod right kidney, there are ultrastructural differences in its cells which reveal its different origin and recent change in function (Andrews, E.B. 1981). The left kidney of caenogastropods is thus a compound organ serving different functions in different parts. It receives a blood filtrate from the heart via the renopericardial canal, alters its composition mainly by processes in the nephridial gland, but to a minor extent elsewhere, and adds nitrogenous excretory material from the dorsal wall. This modified fluid is released to the mantle cavity, probably rhythmically, as demonstrated in the European *Littorina littorea* which discharges urine when first wet by the rising tide (Daguzan 1971). The nature and relative proportions of the nitrogenous end products remain uncertain, but ammonia and uric acid seem the most likely (Duerr 1968). The modified dorsal wall of the kidney in caenogastropods is sometimes referred to as the 'renal gland'. The folded lamellae form a single series in cerithioideans and other neotaenioglossans, but in neogastropods consist of two series of interdigitating lamellae (Perrier 1889; Fretter & Graham 1962; Ponder 1973a).

In *Viviparus* (Drummond 1902) and *Pomatias* (Creek 1951), the renal primordia are reported to be paired at first, but at an early stage, development of the pretorsional left one is arrested; it is incorporated in the reproductive system (Drummond 1902; Otto & Tönniges 1906) or disappears within a few days (Creek 1951; see also Moor 1983). The right kidney of neritopsines is also a remnant associated with the reproductive system, although it still opens to the mantle cavity (Baker 1925; Fretter 1965).

Filtration

Pericardial glands (Perrier 1889; Grobben 1891) are the primary sites of filtration (see Andrews, E.B. 1988 and Fretter & Graham 1994 for reviews) and are composed of tissue including specialised cells (called podocytes) involved in filtration. In patellogastropods, podocytes cover the auricle and ventricle (Ökland 1982), but in fissurellids podocytes are found in a single bay of each auricle close to the openings of the veins (Andrews, E.B. 1985). In most vetigastropods, numerous out-pouchings of the auricular walls form filtration chambers (Andrews, E.B. 1976, 1988) which can be isolated by muscles from the main auricular lumen. At systole, when the ventricle is refilled, blood is retained in these chambers and subjected to pressure, causing fluid and molecules up to a given size to pass through the epicardium to the pericardial cavity. This fluid constitutes the primary urine.

Since the functioning of the heart is dependent on the maintenance of a constant volume of the pericardial cavity (Ramsay 1952; Krijgsman & Divaris 1955), the mechanism for dealing with this production of primary urine is of great importance. The fluid is removed from the cavity by way of ciliated renopericardial canals, which differ in size, that passing to the right kidney being smaller and having shorter cilia than that to the left kidney, suggesting a more restricted flow of primary urine. These canals open rhythmically to the kidneys.

Superficially similar pouches to those seen in vetigastropods are scattered over the auricle in *Viviparus* (Andrews, E.B. 1979, 1988) and ampullariids (Andrews, E.B. 1976) whereas cyclophorids (Andrews, E.B. & Little 1982) lack pouches, but have podocytes on the auricular walls. In most other caenogastropods, an appendage on the inner wall of the auricle is modified as a filtration chamber containing podocytes (Andrews, E.B. 1988). Thus in caenogastropods (including cyclophorids, ampullariids and viviparids), the site of filtration remains primarily the auricular wall (Andrews, E.B. 1988).

Podocytes appear to be absent in heterobranchs (Andrews, E.B. 1988), but few taxa have been investigated in detail. Ultrastructural studies have not been made on neritopsines.

Excretion in Terrestrial and Freshwater Caenogastropods

The excretory organs of terrestrial caenogastropods function to rid the body of nitrogenous waste while conserving water and important ions. These activities have been investigated extensively in only two families, the architaenioglossan Cyclophoridae (Andrews, E.B. & Little 1972, 1982) and the littorinoidean Pomatiastidae (Rumsey 1972; Delhaye 1974), both of which exhibit modifications of the typical plan. In cyclophorids the kidney pore opens to a section of the mantle cavity partly separated from the main cavity, which provides a reservoir from which uptake of water and salts may occur. The filtration chambers in the auricle are reduced in area, cutting the filtration rate and volume, and the kidney can cope with periods of aestivation by storing granules of nitrogenous waste containing calcite, xanthine and potassium urate (Martoja 1975). In the European terrestrial genus *Pomatias* (Creek 1951; Kilian 1951), uric acid accumulates in a so-called concretion gland (perhaps an enlarged area of connective tissue around a blood vessel which is often used for storage). The subsequent fate of this uric acid is uncertain, though this snail contains symbiotic bacteria which may be able to metabolise it in some way.

Nitrogenous excretion in freshwater taxa does not differ markedly from that of their marine relatives. The identity of the nitrogenous waste products is uncertain, especially the relative importance of ammonia, urea, and uric acid (Little 1981). Osmotic interaction with the environment, involving water excretion, salt uptake and solute resorption from the urine, is inevitably of importance as with all freshwater animals, but studies have been confined largely to viviparids and ampullariids (Little 1965a, 1965b, 1979; Delhaye 1974; Andrews, E.B. 1979).

In viviparids, the kidney lies in the mantle skirt, but in ampullariids it is in the base of the visceral mass. In *Viviparus* species, urine output is high, requiring an efficient resorptive mechanism if salts are not to be lost. As in many other freshwater animals, salts can be taken up directly from the external medium and Krogh (1939) recorded uptake from an external concentration as low as 0.1 mM.l^{-1} . Little (1965a, 1965b, 1979) has shown that glucose is resorbed from the primary urine by the walls of the ventricle and that further resorption of small molecules and inorganic ions occurs in the kidney. The pericardial cavity is large, and the kidney is small, an arrangement which allows the former to operate on a constant volume mechanism and the latter to deal with only small quantities of urine, but more effectively. This arrangement is further improved by the fact that the kidney appears to be formed from a hypertrophied nephridial gland (Andrews, E.B. 1979). Resorption is, indeed, the major activity of the kidney, though as shown by Delhaye (1974), a pinocytotic system operating in its cells provides for the ejection of particulate waste. This waste appears not to be nitrogenous, and in the absence of a right kidney, nitrogenous excretion seems here not to have been taken over by the left kidney, but to be accomplished by deposition in connective tissue, elimination by the digestive gland and faeces, and perhaps direct diffusion through external epithelia.

Water and ion balance are dealt with in a different way in the amphibious Ampullariidae. This is not surprising since, unlike many viviparids, they have also to contend with periods of aestivation when water must be conserved. Unexpectedly, perhaps, in view of the need to save salts, the ampullariid kidney has no nephridial gland and resorptive activity is confined to a ureter of pallial origin (Demian & Yousif 1973). Nitrogenous excretion occurs in the kidney and can continue during aestivation, when the organ acts as an accumulation kidney, as it is not simultaneously involved in resorption.

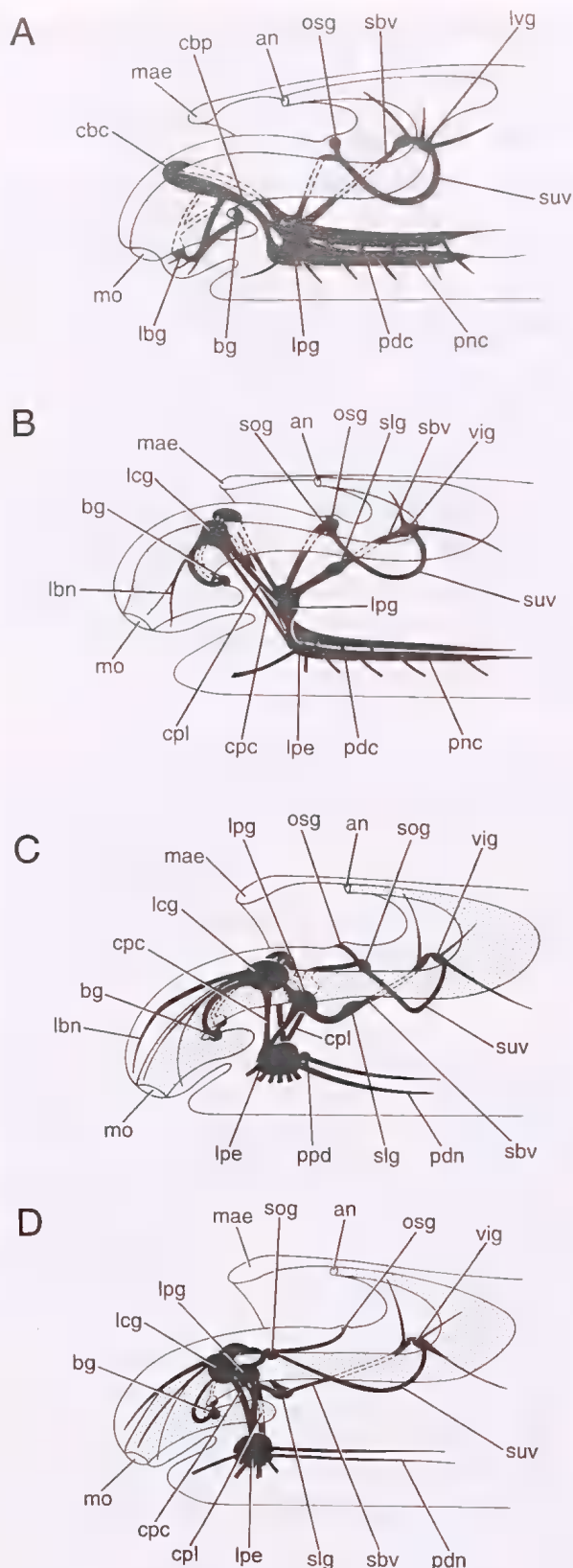


Figure 15.17 Configurations of prosobranch nervous systems. Diagrammatic lateral views of the anterior ends of animals to show: A, an hypoathroid nervous system (for example, Vetigastropoda); B, a dystenoid nervous system (for example, *Viviparus*, an architaenioglossan caenogastropod); C, an epiathroid nervous system (for example, most caenogastropods (Sorbeoconcha)); D, a concentrated nervous system (higher caenogastropods). an, anus; bg, buccal ganglion; cbc, cerebral commissure; cbp, cerebropleural connective; cpc, cerebropleural connective; cpl, cerebropleural connective; lbg, labial ganglion; lbn, labial nerve; lcg, left cerebral ganglion; lpe, left pedal ganglion; lpg, left pleural ganglion; lvg, left visceral ganglion; mae, mantle edge; mo, mouth; osg, oesophageal ganglion; pdc, pedal commissure; pdn, pedal nerve; pnc, pedal nerve cord; ppd, postpedal commissure; sbv, suboesophageal part of visceral loop; sig, suboesophageal ganglion; sog, supra-oesophageal ganglion; suv, supra-oesophageal part of visceral loop; vig, visceral ganglia. (Modified after Fretter & Graham 1962)

[I. Hallam]

The Nervous System and Sense Organs

There are two main configurations of gastropod nervous systems: hypoathroid and epiathroid. In the hypoathroid condition (Fig. 15.17A), the pleural and pedal ganglia are closely associated and well separated from the cerebral ganglia, whereas in the epiathroid condition (Fig. 15.17C, D) the pleural and cerebral ganglia are closely associated. Patellogastropods, vetigastropods (Figs. 14.13A, 15.18) and neritopsines all have hypoathroid nervous systems, which is presumably the primitive condition. At the lower end of the caenogastropod clade the Cyclophoridae and Ampullariidae also have hypoathroid nervous systems and the Viviparidae have an intermediate condition known as dystenoid (Fig. 15.17B; Fretter & Graham 1962). All other caenogastropods have epiathroid nervous systems (Fig. 15.17C, D), as do many heterobranchs. Haszprunar (1985a, 1988a, 1988b, 1993) regarded architaenioglossans as 'archaeogastropods' because of their hypoathroid nervous system, arguing that the epiathroid condition evolved only once, and was present in the common ancestor of caenogastropods and heterobranchs. Ponder (1991a) argued that the epiathroid condition probably arose independently in both groups, a view supported by recent cladistic analyses (Ponder & Lindberg 1996, 1997).

Other trends include concentration of the circumoesophageal nerve ring so that the ganglia are brought closer together (Fig. 15.17D) or even fuse, and shortening of the visceral nerve loop. Linkages improving neural coordination and control are obtained by zygoneury, a connection between the right pleural and suboesophageal ganglia or between left pleural and supra-oesophageal ganglia, and dialyoneury, a connection between the left and right pallial nerves.

Pedal nerve cords occur as a primitive character state in gastropods; caenogastropods generally have none, although they are found in cypraeids (Bouvier 1887). The nerve ring lies anterior to the buccal mass in Patellogastropoda, most Vetigastropoda and Neritopsina (and most Heterobranchia). Posterior migration has occurred in a few vetigastropods and most caenogastropods (and in a few opisthobranchs). Many pedal nerves arise from the anterior end of the pedal ganglia in caenogastropods, including architaenioglossans, but few in other gastropods (Ponder & Lindberg 1997). In addition, innervation of various organs, in particular the pallial organs, differs in detail from group to group.

The Nervous System of *Calliostoma*

The nervous system of *Calliostoma* is illustrated in Figure 15.18. The cerebral ganglia lie dorso-lateral to the anterior region of the buccal cavity and are united by a long commissure which encircles the head anteriorly. Nerves from the cerebral ganglia innervate the snout, tentacles, eyes and statocysts. From each ganglion a connective arises ventrally and, after passing postero-dorsally for a short distance, enters the buccal musculature near the origin of the radular sac where it joins the buccal ganglion. A commissure links the two buccal ganglia. Near the point where each buccal connective originates in the cerebral ganglion, a nerve branches to the odontophore. Just before joining the buccal ganglia, each buccal connective gives off a stout branch which runs beneath the anterior end of the oral tube and contains numerous nerve cells. These are the somewhat ill-defined labial ganglia which are joined by a narrow commissure. From them nerves pass to the lips and the muscles of the buccal wall. The buccal ganglia innervate the radular membrane and muscles of the radular sac, the salivary and oesophageal glands, the walls of the buccal cavity and the oesophageal valve.

The cerebropleural and cerebropleural connectives arise from the postero-ventral surface of each cerebral ganglion and run backwards into the anterior part of the foot where they connect with the paired pleural and pedal ganglia respectively. The pedal ganglia are the largest and most ventrally placed. They extend posteriorly through the foot as elongate pedal cords and are connected by transverse commissures which are shorter and

thicker anteriorly. The pedal ganglia give off numerous ventral and lateral nerves and, anteriorly, a pair of stout epipodial nerves. The pleural ganglia are fused to the dorsal surface of the pedal ganglia and innervate the mantle, a nerve from each passing to a circum-pallial nerve at the mantle edge.

The remainder of the central part of the nervous system consists of the visceral loop which arises from the pleural ganglia. The supra-oesophageal connective runs from the right pleural ganglion dorsally over the mid-oesophagus. It gives rise to small branches to the body wall as it approaches the ctenidium on the left, where it passes into the body wall to the relatively small supra-oesophageal ganglion, from which a nerve passes to the branchial ganglion. Before entering the branchial ganglion the nerve forms an anastomosis with the left pallial nerve, a condition known as dialyneury. Nerves from the branchial ganglion innervate the ctenidium and osphradium. The supra-oesophageal visceral connective arises from the supra-oesophageal ganglion and passes back through the haemocoel to the visceral ganglion situated near the origin of the transverse pallial vein. The suboesophageal connective arising from the left pleural ganglion leads back beneath the oesophagus and the radular sac to join the visceral ganglion; there is no ganglion along its course. Half way along its length the suboesophageal connective anastomoses with the right pallial nerve by way of a very fine connection. Three nerves are given off from the visceral ganglion: a renal nerve which branches to each kidney, a visceral nerve travelling up the visceral mass and innervating the stomach, the digestive gland and gonad, and a pericardial nerve.

The nervous system in *Calliostoma* (and other vetigastropods) shows several primitive features not seen in many other gastropods. The cerebral ganglia are situated anteriorly, whereas in most caenogastropods the nerve ring lies behind the buccal mass. Labial ganglia and a labial commissure are present, but have been lost in caenogastropods and heterobranchs. The pleural ganglia are in a ventral, hypoathroid position. The pedal cords and numerous pedal commissures are elongate, whereas most caenogastropods and all heterobranchs have a distinct pedal ganglion and lack pedal cords (Fig. 15.17C, D). Nerve cells are not confined to the ganglia – all non-vetigastropods have the nerves confined to the ganglia and, related to this condition, nerves originate from the visceral loop in vetigastropods, but originate from the ganglia in other groups.

Sense Organs

The vetigastropod head is well endowed with sensory structures. The oral margin is fringed with papillae and a pair of long, tapering, cephalic tentacles, covered laterally with sensory papillae (Fig. 15.20), arise from the base of the snout. On the inner side at the base of each tentacle is a small cephalic lappet of unknown function, presumably sensory; and lateral to each tentacle is a narrow eye stalk. The eye is a deep, pigmented pit, its opening plugged by a cuticular lens (Fig. 15.19B). The foot is fringed with epipodial tentacles covered with sensory papillae; some of these tentacles have an epipodial sense organ at the base. Several of the above structures are external – including the eyes, cephalic tentacles, sensory papillae, epipodial tentacles and epipodial sense organs – but others, the bursicles, osphradium and subradular organ, are internal in the mantle cavity although in direct contact with external stimuli. The statocysts are completely internal, and are responsive to gravity.

Eyes

In patellogastropods, the eyes are placed laterally, at the outer bases of the cephalic tentacles, but in vetigastropods, neritopsines and architaenioglossans the eyes are located on separate peduncles on the outer sides of the tentacle bases. A peduncle is absent in higher caenogastropods (for example, Strombidae) but the eyes are raised from the head in neogastropods and a few other caenogastropods by the extension of the tentacle bases so that the eye is distal to the base along the tentacle.

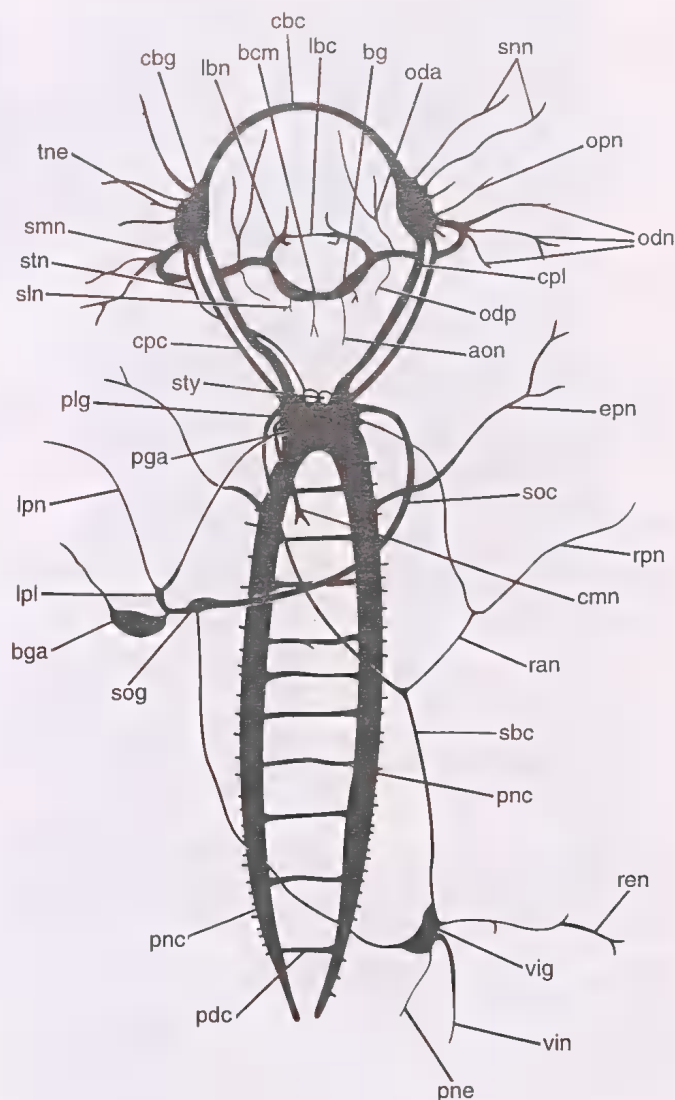


Figure 15.18. Nervous system of *Calliostoma zizyphinum* (Trochidae). aon, nerve to anterior oesophagus; bcm, buccal commissure; bg, buccal ganglion; bga, branchial ganglion; cbc, cerebral commissure; cbg, cerebral ganglion; cmn, nerve to columellar muscle; cpc, cerebropleural connective; cpl, cerebropleural connective; epn, epipodial nerve; lbc, labial commissure; lbn, labial nerve; lpl, left pallial anastomosis; lpn, left pallial nerve; oda, nerve to anterior part of odontophore; odn, nerves to odontophore; odp, nerve to posterior part of odontophore; opn, optic nerve; pdc, pedal (transverse) commissure; pga, pedal ganglion; plg, pleural ganglion; pnc, pedal nerve cord; pne, pericardial nerve; ran, right pallial anastomosis; ren, renal nerve; rpn, right pallial nerve; sbc, suboesophageal connective; sln, salivary nerve; smn, stomatogastric nerve; snn, nerves to snout; soc, supra-oesophageal connective; sog, supra-oesophageal ganglion; stn, statocyst nerve; sty, statocyst; tne, tentacular nerve; vig, visceral ganglion; vin, visceral nerve (or pedal nerve). (After sketch by A. Graham) [B. Scott]

The most primitive eyes are found in patellogastropods (Fig. 15.19A), which have an open vesicle lacking a lens (Marshall & Hodgson 1990). In many Vetigastropoda (as in *Calliostoma*), the eyes are narrowly open, but have a lens (Fig. 15.19B). Neritopsines, fissurellids, caenogastropods and heterobranchs have closed eyes with a lens (Fig. 15.19C).

Cephalic Tentacles

The cephalic tentacles are among the most important prosobranch sense organs, although little attention has been paid to their fine structure and function. They are richly endowed with sensory cells which may be significantly different in each of the major groups of gastropods (Storch & Welsch 1969; Haszprunar 1988a; Marshall & Hodgson 1990; Voltzow 1994).

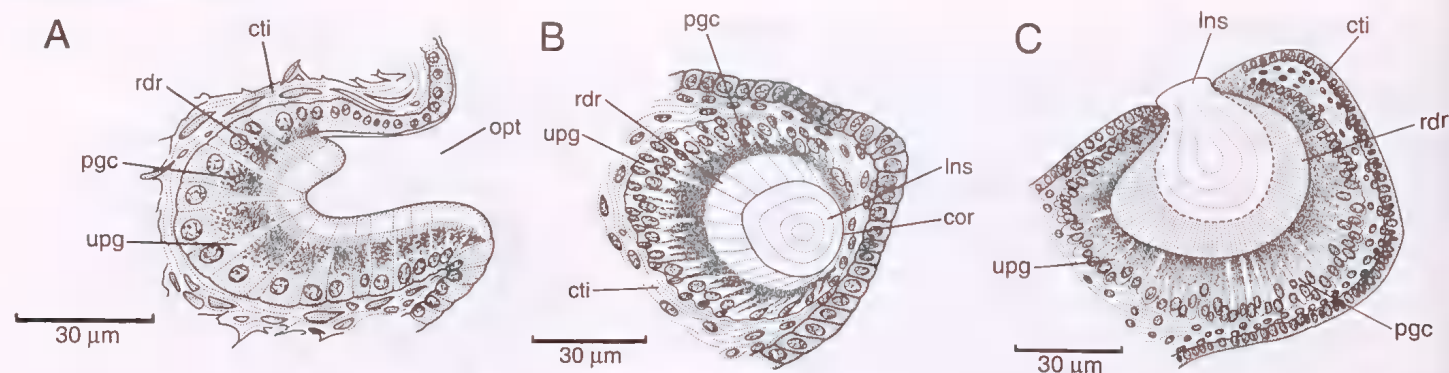


Figure 15.19 Prosobranch eyes, in vertical section. **A**, *Patella vulgata* (Patellogastropoda, Patellidae). **B**, *Trichotropis borealis* (Caenogastropoda, Capulidae). **C**, *Cantharidus clelandi* (Vetigastropoda, Trochidae). cor, cornea; cti, connective tissue; lns, lens; opt, opening of optic cup; pgc, pigment cell of retina; rdr, rod of retinal cell; upg, unpigmented cell of retina. (After Fretter & Graham 1962)

Statocysts

Statocysts are found in most gastropods where they are associated with the pedal ganglia, although innervated by the cerebral ganglia. In patellogastropods, they lie lateral to the pedal ganglia (Thiem 1917; Stützel 1984). In other gastropods they lie either anterior to the pedal ganglia, dorsal to them or just behind them (Ponder & Lindberg 1997). Each statocyst contains either many statoconia, as in most lower 'prosobranchs' and heterobranchs, or only a single statolith as in many caenogastropods.

Osphradium

The position of the osphradium is constant in the main groups of gastropods (Haszprunar 1988a). It occurs on the pallial floor in patellogastropods, but on the pallial roof of all other gastropods (Haszprunar 1988a). In vetigastropods, it is located on the efferent branchial membranes. The fine structure of the osphradium has received considerable attention (Welsch & Storch 1969; Crisp 1973; Haszprunar 1985a, 1985b; Taylor, J.D. & Miller 1989) and the details are diagnostic of higher groups. For example, 'cilia bottles' are found only in some vetigastropods (Haszprunar 1985a). They are situated close to the edge of the sensory area and have a fluid-filled lumen containing special cilia. Haszprunar (1985a) has shown that the distinctive Si1, Si2 and Si4 cells (Welsch & Storch 1969) are a synapomorphy of caenogastropods (excluding architaenioglossans).

The osphradium is small in most gastropod groups, but is large and well developed in many caenogastropods where the surface area is increased by elongation or folding; leaflets are formed in several groups (Haszprunar 1985a; Maeda 1986; Taylor, J.D. & Miller 1989). Ciliated lateral fields are present on the osphradia of Neritopsina, Cerithioidea, Neotaenioglossa and Neogastropoda (Haszprunar 1985a), but are formed in a different way in each group.

Bursicles

Bursicles, or ctenidial sense organs, are sensory pockets near the base of the efferent edge of each ctenidial leaflet. Their structure has been described by Szal (1971) and Haszprunar (1987b). They are a synapomorphy of vetigastropods (Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a; Ponder & Lindberg 1997). They possibly function as distance chemoreceptors (Szal 1971), and are possibly significant in predator detection.

Subradular Organ

The subradular organ, or licker, can be protruded from the mouth and apparently is used to sense potential food. In gastropods, it occurs in patellogastropods (Hyman 1967; Fretter & Graham 1994), *Haliois* (Fleure 1905), fissurellids (Haller 1884), peltospirids (Fretter 1989) and ampullariids (Lutfy & Demian 1967). It is located in the ventral subradular (or sublingual) pouch, which opens to the anterior buccal cavity and is a modification of the mid-dorsal epithelium. The gastropod subradular organ has

received little attention, the only studies being those of Hyman (1967) and Salvini-Plawen (1988). A labial commissure, sometimes with labial ganglia, usually innervates the subradular organ. However, the commissure and ganglia are not associated with the subradular organ in ampullariids and peltospirids. The commissure is also present in polyplacophorans (Eernisse & Reynolds 1994), monoplacophorans (Lemche & Wingstrand 1959), *Nautilus* and scaphopods (Salvini-Plawen 1988) and is considered plesiomorphic in Gastropoda.

Sensory Papillae

Sensory papillae (Crisp 1981; Marshall & Hodgson 1990) occur on the cephalic (Fig. 15.20) and epipodial tentacles (and on the mantle and foot in some taxa) in Vetigastropoda, and appear to be apomorphic in the group (Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a). They form 'seta'-like projections on the cephalic and epipodial tentacles. Each papilla is a truncated cone covered with microvilli and with an apical crown of short, stout cilia encircling a central dome of microvilli from which project two or three shorter cilia. The sensory cilia originate from the terminations of sensory dendrites within the papilla (Herbert 1984). Ciliary bundles are also found on the cephalic tentacles of patellogastropods (Marshall & Hodgson 1990) and although these may be homologous with vetigastropod papillae, they are not raised into papillae.

Epipodial Sense Organs

First described by Crisp (1981), these structures lie at the bases of the epipodial tentacles of vetigastropods and are synapomorphic for vetigastropods (Haszprunar 1988a). Haszprunar (1985g) contrasted them with other innervated molluscan sense organs that have collar receptors.

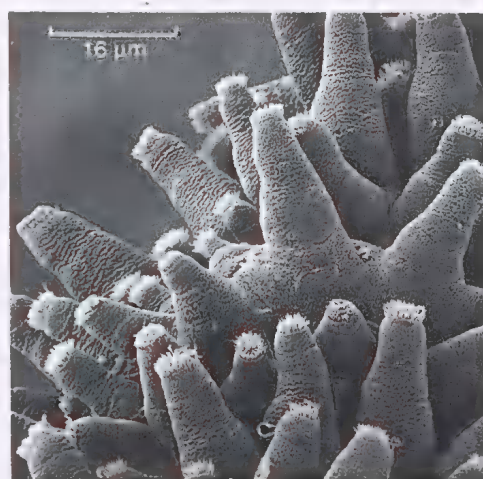


Figure 15.20 Sensory papillae on a cephalic tentacle of *Gibbula umbilicalis* (Vetigastropoda, Trochidae). (D.G. Herbert)

Reproduction

The Reproductive System of *Calliostoma*

Like other trochoideans and most other streptoneuran gastropods, species of *Calliostoma* are gonochoristic (have separate sexes). The gonad spreads along the columellar side of the visceral coil, the testis pinkish white and the ovary greenish. The short gonadial duct opens to the duct of the right kidney near the opening of the renopericardial canal. The right kidney opening is thus urinogenital and in females it is at the end of a prominent glandular papilla (Fig. 15.8) derived from the posterior part of the right hypobranchial gland. Eggs discharged from the ovary measure about 280 μm in diameter and each is enclosed in a gelatinous secretion ('egg layer' or 'egg envelope'; see Fretter & Graham 1962, fig. 166; Dohmen 1983) derived from the ovum. The egg layer swells in contact with sea water; this layer occurs in most vetigastropods, but is absent in other gastropods.

When males and females of a trochoidean like *Calliostoma zizyphinum* come together in the breeding season and simultaneously discharge gametes, several hundred eggs are liberated at each spawning. In some species, such as *C. zizyphinum*, the eggs are not discharged into the sea, but are fertilised within the mantle cavity as they are entangled in secretion from the glandular papilla. An egg ribbon emerges from the cavity (Fig. 15.21) and is attached to the substratum by the foot, the outer secretion hardening on contact with sea water. The embryos take about a week to pass through trochophore and veliger larval stages before the young emerge from the disintegrating ribbon as miniatures of the adult, having used up the yolk and fed on the jelly in which each ovum is embedded (Lebour 1937; Crofts 1955).

Reproduction and Gonoducts

The majority of 'prosobranch' gastropods are, like trochoideans, gonochoristic and have only the post-torsional right gonad. Most have a coiled shell and the gonad and digestive gland fill most of the coils, the gonad mainly on the columellar side, though in some viviparids the testis spreads into the mantle skirt (von Rohrbach 1937; Berry 1974). In contrast, the gonad of patellogastropods lies ventrally between the rest of the visceral mass and the foot and when ripe extends dorsally on the left side. In basal gastropods the gonoduct is entirely mesodermal and connects directly with the kidney. In neritopsines and caenogastropods, the gonoducts are a mixture of mesoderm (including the incorporation of the right kidney into the 'renal gonoduct', a short tube between the gonadial tube and the ectodermal part of the gonoduct) and ectoderm, much of the distal part of the duct lying in the pallial wall.

Fertilisation is external in most patellogastropods and vetigastropods, though it may occur in the mantle cavity, and most have pelagic development (Fretter & Graham 1962; Fretter 1984b; Hickman 1992). With the exception of a few groups like lepetodriloid hot-vent limpets (Fretter 1988), male and female systems of gonochoristic vetigastropods and patellogastropods are similar in general plan (Fig. 15.22A). Tubules of the gonad join to form a short gonadial duct discharging to the right kidney not far from its opening; the lip of the urinogenital opening, especially in females, may have conspicuous glandular elaborations like that of *Calliostoma*. Some trochids shed their eggs singly and secretions from the rosette-shaped lips of the urinogenital opening (Fig. 15.22A) and hypobranchial gland entangle them as they pass through the mantle cavity and become planktonic. In others the spawn is fixed either by agglutination of the egg coverings (for example, in the European fissurellid genus *Diodora* and trochid *Gibbula tumida*; Fretter & Graham 1994) or by secretion from a glandular section of the female urinogenital duct. The latter either forms a prominent papilla (as in the European trochid *Margarites*), or lies in the thickness of the right hypobranchial gland as in *Pleurotomaria* (Fretter 1966) and some trochids (for example, *Calliostoma* and *Jujubinus*).



Figure 15.21 Spawn ribbon emerging over the right neck lobe of *Calliostoma zizyphinum* (Vetigastropoda, Trochidae). [P. Bouchet]

Although primitive taxa have external fertilisation and pelagic, non-feeding larvae, more highly derived taxa, including some freshwater and terrestrial species, have internal fertilisation, the addition of a non-pelagic phase within an egg capsule or brood pouch, and feeding larvae. Neritopsines, caenogastropods and heterobranchs show all of these trends, as do vetigastropods, with the exception of feeding larvae. Thus internal fertilisation with the associated changes in the reproductive systems, occurs in only a few patellogastropods and vetigastropods, but is found in all Neritopsina, Cocculinioidea and Caenogastropoda. It is usually achieved with a copulatory structure (penis), but several groups use spermatophores (Robertson 1989). The aphallate ptenoglossans produce spermatzeugmata comprising paraspermatozoa modified to carry typical euspermatozoa.

A few patellogastropods (Golikov & Kussakin 1972; Lindberg 1983) have evolved copulatory structures and internal fertilisation independently. Similarly, some vetigastropods – several trochoideans and Seguenzioidea (Quinn 1983a, 1991) – and Lepetelloidea (Haszprunar 1987c, 1988c, 1988d) and cocculinioideans (Haszprunar 1987a, 1988c) have pallial genital structures and some have penes derived from a variety of appendages. In the vetigastropod hot-vent limpet *Lepetodrilus* (Fretter 1988), the length of the testicular duct approaches that of caenogastropods; the duct also functions as a seminal vesicle. It opens to a conducting part of the right kidney leading to the urinogenital aperture; there is a pallial prostate and an epipodial penis on the right side of the head, each with a seminal groove. In the related genus *Gorgoleptis*, the penis, on the left side of the snout, appears to act as a pipette, transferring sperm from the genital opening of the male to that of the female (Fretter 1988). Members of another hot-vent group, the Peltospiridae (Fretter 1989; McLean 1989a), are aphallic; sperm liberated by the male make their way to the ovarian tubules via a receptacular duct and fertilisation is in the ovary. In the hot-vent taxon *Neomphalus*, there are also complex glandular pallial genital ducts and the male bears a penis on the left side of the head (Fretter *et al.* 1981).

In caenogastropods (Fig. 15.22C–E) and neritopsines (Fig. 15.22B), eggs or sperm pass into a glandular duct running along the right mantle wall and fertilisation is internal. In the male, the sperm pass through the duct, which typically is at least in part a prostate gland (Fig. 15.22F, H). In the female, eggs receive protective coatings following fertilisation, and in a few species, are retained to be incubated.

15. PROSOBRANCHS

The manufacture of spawn masses or egg capsules is correlated with the hypertrophy of glands associated with the oviduct. Typically, there is a proximal albumen gland (Fig. 15.22B–E) and a distal jelly or capsule gland. The eggs are fertilised in the proximal end of the pallial duct. As they pass along the duct, secretions are distributed by cilia and moulded around the eggs by muscles which also regulate the passage of the eggs. In contrast to the male gonadial duct, that of the female is straight, and long, and a gonopericardial canal is more common. Species with aphyallic males usually have a long opening to the pallial oviduct (cerithioideans, most ptenoglossans, vermetids, eatoniellids), often extending most of the length of the duct, although aphyallate cingulopsids (Fretter & Patil 1958; Ponder 1968a) have a closed pallial oviduct. Most phallate species have a closed pallial oviduct. It is open in others such as eulimids (Ponder & Gooding 1978; Warén 1983a, 1983b), a few hydrobiids (for example, *Ascorhis*, Ponder & Clark 1988) and some rissoiids (Ponder 1985a). Species of *Trivia* (Fig. 15.22E; Fretter 1946), *Velutina* and *Erato* (Fretter 1951b) also have a long pallial opening to the oviduct gland.

The open pallial genital ducts seen in some caenogastropods might be regarded as primitive partly because during development they first appear as a groove along the right margin of the mantle skirt and later close (Johansson 1950). However, the open condition also occurs in species with many derived characters, suggesting that at least in some cases it could be secondary. Some species with egg capsules that are large relative to the size of the snail also have an extensive oviducal opening to the mantle cavity as in the European terrestrial littorinoidean genus *Pomatias* (Creek 1951). Kostitzine (1949) has shown that the site of closure in young *Nucella* species is marked by a ciliated ventral channel, a characteristic of the female pallial duct of many other caenogastropods, and the sperm pouches are associated with this channel. There may be a pouch at each end, a distal bursa and proximal receptaculum as in species of *Littorina* (Fig. 15.22C), stenoglossans and some toxoglossans, or both may be proximal, as in most rissooideans (Ponder 1988a). In the first arrangement, the channel is sperm-conducting, in the second vaginal. In some rissooideans (Ponder 1988a), such as pomatiopsids (Dundee 1957; Davis 1979), and also in some neritoideans (Houston 1990), the vaginal channel is separated from the rest of the pallial duct; in the first it may share the genital aperture, whereas others, including some neritoideans (Fig. 5.19B), are diallic. Some other neritids are triaulic, having a third duct, the ductus enigmaticus of Bourne (1908), related to the bursa and receptaculum, which carries waste to the mantle cavity. The right kidney of neritopsines and caenogastropods is incorporated into the genital system. In neritopsines, the pallial section of the duct develops within the anterior pallial vein alongside the rectum (Fretter 1965) and is more complex than the pallial duct of gonochoristic caenogastropods.

Internal fertilisation in caenogastropods is associated with the development of pouches on the female duct for receiving (bursa copulatrix) and storing sperm (seminal receptacle) and in some species there is a gland for ingesting spent or excess sperm (Fretter 1941; Fretter & Graham 1962). These glandular parts of the reproductive system (prostate gland, oviduct glands) and sperm sacs, such as bursa copulatrix and seminal vesicle are of uncertain homology across major groups. Even within related groups, homologies are often uncertain (for example, the bursa copulatrix in the Rissooidea, Ponder 1988a). The testicular duct (Fig. 15.22H), typically long, runs superficially along the columellar side of the visceral mass and with few exceptions (for example, some Columbellidae, Marcus, Er. & Marcus, Ev. 1962) acts as a seminal vesicle. It is coiled to increase the surface area, although exceptionally this is achieved by the development of branching tubules, as in the New Zealand volute *Alcithoe* (Ponder 1970b). Ingestion of spent or superfluous sperm by its epithelium is reported in some genera for example, *Littorina* (Linke 1933), *Melanopsis* (Bilgin 1973), muricoideans (Fretter 1941; Ponder 1972a) and turrids (Smith, E.H. 1967c). A sphincter separates this duct from the renal vas deferens which in a few

species is linked to the pericardium by a gonopericardial duct (for example, *Oenopota turricula*, Smith, E.H. 1967c; volutomitrids, Ponder 1972a) or a dense strand of connective tissue.

When present, the copulatory structure (penis or verge) in most caenogastropods is situated at the base of the head, usually behind the right cephalic tentacle. As in all phallate streptoneuran gastropods, the penis is muscular, vascular and non-invaginate and when gorged with blood its size may double. The penis may be formed from cephalic tissue (for example, Lottiidae, Golikov & Kussakin 1972; *Neomphalus*, Fretter *et al.* 1981; neritids, Fretter 1984b), epipodial tissue (for example, Seguenziidae, Quinn 1991; Lepetodriloidae, Fretter 1988), or the propodium (Skeneidae, Warén & Bouchet 1993). In many cocculiniform limpets (Haszprunar 1988c) and *Choristella* (Haszprunar 1990), the right cephalic tentacle is used in copulation and in *Cocculina* a penis arises from the right side of the foot (Thiele 1929–1935; Haszprunar 1987a). Although the copulatory organ usually lies on the right side, in a few taxa (for example, *Neomphalus*, Fretter *et al.* 1981) it is on the left.

In basal caenogastropods (architaenioglossans), the penis is derived differently in various groups. In Ampullariidae, it originates from the pallial edge (Andrews, E.B. 1964; Berthold 1991) and in viviparids from a modified right tentacle. Cyclophoroidea have the penis behind the right tentacle, innervated from the right pleural ganglion (Kretzschmar 1919). In most 'higher' caenogastropods, the penis is pedally innervated. Exceptionally, for example in anabathrids and emblemidids, the penis is cerebrally innervated (Ponder 1988a), suggesting independent origins in some groups; further support for this derives from the fact that several groups lack penes (Cerithioidea, non-eulimid ptenoglossans, Cingulopsoidea). Unlike other neogastropods, in columbellids (Marcus, Er. & Marcus, Ev. 1962) the penis is slotted into a pouch within the hypobranchial gland when at rest. Glands producing secretions which hold the penis in position during copulation are scattered, or concentrated to form mamilliform structures, as in many littorinids (Linke 1933; Heller 1975; Reid 1989a) and rissooideans (for example, hydrobiids, Thompson 1968; *Caecum*, Götze 1938; Marcus, Er. & Marcus, Ev. 1963; *Rissoina*, Ponder 1968a, 1985a). These glands may disappear seasonally, as in the European *Littorina littorea* (Linke 1933). The penis of the planktonic heteropods has a flagellum and glands to secure a hold on the partner; body position is maintained by a pedal sucker.

Those caenogastropod groups that are aphyallic mostly have an open male pallial duct with broad glandular lamellae extending to the mouth of the mantle cavity (for example, Turritellidae, Cerithiidae, Vermetidae, Cerithiopsidae), though in the siliquariid genus *Stephopoma*, the opening of the vas deferens is far back in the mantle cavity and sperm leave the body by way of the food groove (Morton J.E. 1951b, 1951c, 1951d).

A prostate gland, typically associated with the pallial vas deferens, may comprise epithelial gland cells alternating with ciliated cells lining a narrow tube, or the gland cells may thicken the wall on each side of the original groove (Fig. 15.22F, H). In most species the duct closes and discharges to a muscular, ciliated duct passing to the penis, although in others it is open throughout its length (littorinids, strombids, lamellariids, naticids, eulimids) or only in the pallial section (for example in the volute *Alcithoe*, Ponder 1970b). Often, in an otherwise closed duct, a small posterior opening to the mantle cavity remains (Fig. 15.22H). Some neritids have no duct linking the pallial duct with the penis, but a groove along the overlying mantle, as in *Theodoxus* (Fretter 1946), or along the body wall as in *Phenacolepas* (Fretter 1984a). Other variations relate to glandular structures. A prostate gland may not be developed (some columbellids, Marcus, Er. & Marcus, Ev. 1962) or, in genera in which it does not form thick lamellae, its secretion is typically augmented by glands opening to the penial duct (for example, *Nassarius*, Fretter & Graham 1962; some marginellids, Ponder 1970a; *Rissoa*, Fig. 15.22G, Ponder 1985a; some anabathrids, Ponder 1983a; and some volutomitrids, Ponder 1972a).

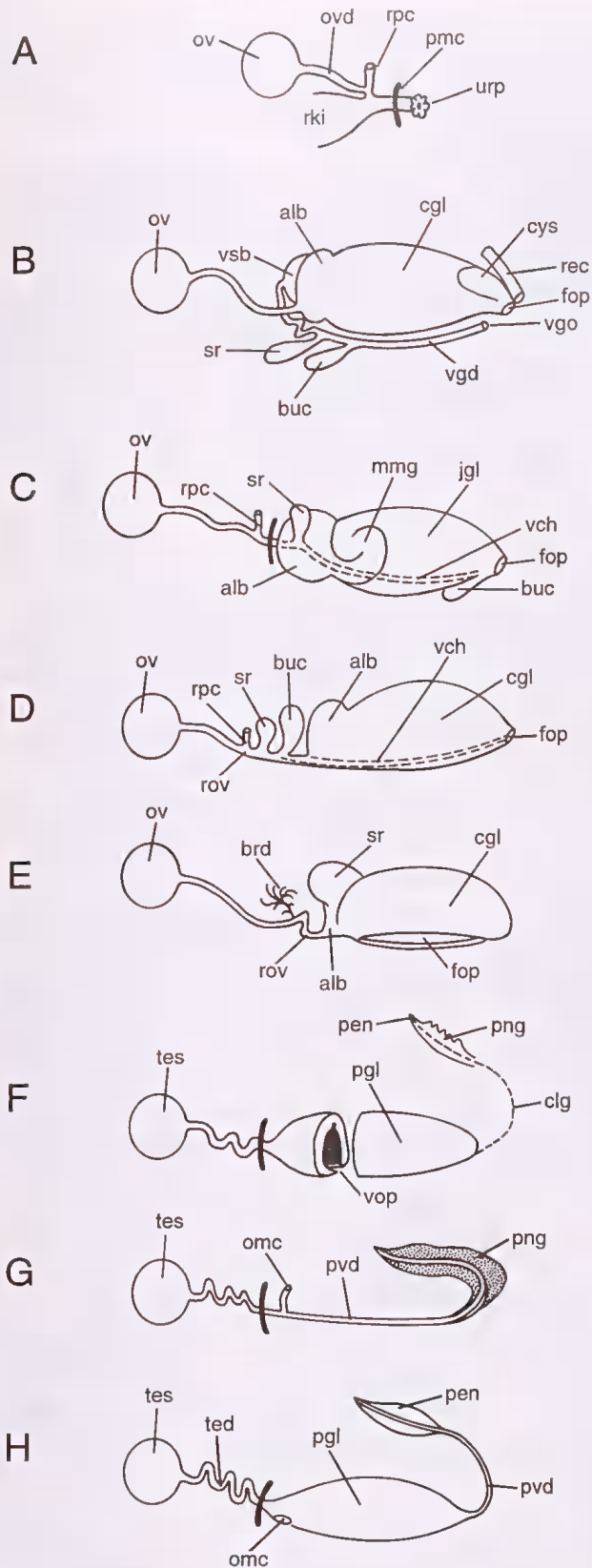


Figure 15.22 Prosobranch genital ducts, comparative diagrams: A–E, female; F–H, male. A, a trochid (Veligastropoda) that broadcasts gametes; B, *Theodoxus* (Neritopsina, Neritidae); C, a littorinid that produces an egg mass (Caenogastropoda); D, a hydrobiid (Caenogastropoda); E, *Trivia monacha* (Caenogastropoda, Triviidae); F, a littorinid (Caenogastropoda); G, *Rissoa parva* (Caenogastropoda, Rissoidae); H, a stenoglossan neogastropod (Caenogastropoda). alb, albumen gland; brd, branching duct in which superfluous sperm are ingested by amoebocytes; buc, bursa copulatrix; cgl, capsule gland; clg, ciliated groove; cys, crystal sac; fop, female opening; jgl, jelly gland; mmg, membrane gland; omc, opening to mantle cavity; ov, ovary; ovd, ovarian duct; pen, penis; pgl, prostate gland; pmc, posterior limit of mantle cavity; png, penial gland; pvd, pallial vas deferens; rec, rectum; rki, right kidney; rovd, renal oviduct; rpc, renopericardial duct; sr, seminal receptacle; ted, testicular duct; tes, testis; urp, urinogenital papilla with glandular lips; vch, ventral channel; vgd, vaginal duct; vgo, vaginal opening; vop, ventral opening of prostate; vsb, vestibule. (Modified after Fretter & Graham 1962) [D. Wahl]

Hermaphrodites

Relatively few streptoneuran gastropods are simultaneous hermaphrodites. Most of those traditionally referred to as such are heterobranchs, among them pyramidellids, valvatids and rissoellids. However, several are hermaphroditic, including cocculinoideans (Haszprunar 1988c), some lamelliariids (Fretter & Graham 1962), some eulimids (Fretter 1984b), and perhaps the fissurellid *Puncturella noachina* (Rammelmeyer 1925). Rarely, eggs and sperm are produced in different lobes (acini) of the same gonad (for example, *Velutina*). More usually, the testis and ovary are separate, each with its own gonadal duct as in the eulimid genus *Goodingia* (Lützen 1972). These differences, and others related to the pallial ducts, indicate that simultaneous hermaphroditism has arisen independently in a number of groups. Consecutive hermaphroditism is more widespread and usually involves a single change from male to female. Among the caenogastropods, it occurs in members of the Hipponicoidea, Calyptraeidea, Ptenoglossa, Eulimidae and in the littorinid *Mainwaringia* (Reid 1986a), a vitrinellid (Bieler & Mikkelsen 1988) and the turrid *Oenopota turricula* (Smith, E.H. 1967c). Multiple protandrous hermaphroditism, where several consecutive sex changes occur, has been reported in the ptenoglossans *Janthina* (Laursen 1953) and *Epitonium clathrus* (Ankel 1936b).

A number of patellogastropods are protandrous consecutive hermaphrodites (Orton 1920; Orton, Southward & Dodd 1956; Fretter & Graham 1962), but, except for *Probalacmaea*, in which a penis has been described (Thorson 1935; Golikov & Kussakin 1972), it affects only the gonad. In *Patella*, the gonad of immature individuals contains oogonia and spermatogonia (Choquet 1970). Sex change may occur after a single breeding season or, more commonly, after two or three seasons, occasionally later, but in some individuals it never occurs. Sex change is also known to occur in the fissurellid genus *Diodora* (Bacci 1947).

In protandrous caenogastropods, changes in the pallial ducts accompany the sex change, although these may be slight. In the aphyllid genus *Epitonium*, both sexes have an open glandular duct and the sex change involves the development of a receptaculum and hypertrophy of the glands (Ankel 1936b). In *Janthina*, also aphyllid, but with a closed duct, a tubular gland at the inner end of the prostate becomes the albumen gland and the prostate becomes the mucous gland (Graham 1954a). In calyptraeids (Giese 1915) and capulids (Graham 1954b; Yonge 1962), the pallial vas deferens is an open groove continuous with the groove leading to the penis. In the female phase, the pallial groove is closed and its walls enlarge to form albumen and capsule glands and a receptaculum, and the anterior groove is lost. The penis is lost in *Calyptraea* (Giese 1915) and in the capulid *Trichotropis borealis* (Graham 1954b), but is reduced in the female phase in *Capulus* (Giese 1915). The only species reported in which the testicular duct is not converted into the oviduct are *Stilifer linckiae* (Lützen 1972), *Oenopota turricula* (Smith, E.H. 1967c, 1967d) and *Mainwaringia* (Reid 1986a).

The timing of sex reversal in some genera is primarily under genetic control and is unaffected by external stimuli. It typically occurs at the end of the first breeding season – in *Calyptraea* (Bacci 1951); *Capulus* (Giese 1915); *Trichotropis* (Graham 1954b; Yonge 1962); and *Eulima* and *Niso* (Warén 1983a). In others it depends on external stimuli and can be a response to the particular substratum on which the larva settles, as in some eulimids (Lützen 1972; Warén 1983a), in *Crucibulum* (Coe 1938) and *Crepidula* species (Conklin 1897; Coe 1938; Walne 1956; Hoagland 1978). In *Crepidula*, the presence of a female will prolong the male phase (Coe 1944) and this may also be the case in the hipponicid *Sabia australis* (Laws 1970; Knudsen 1991). In some territorial patellogastropods sex change is dependent upon acquisition of a territory (Wright & Lindberg 1982; Lindberg & Wright 1985).

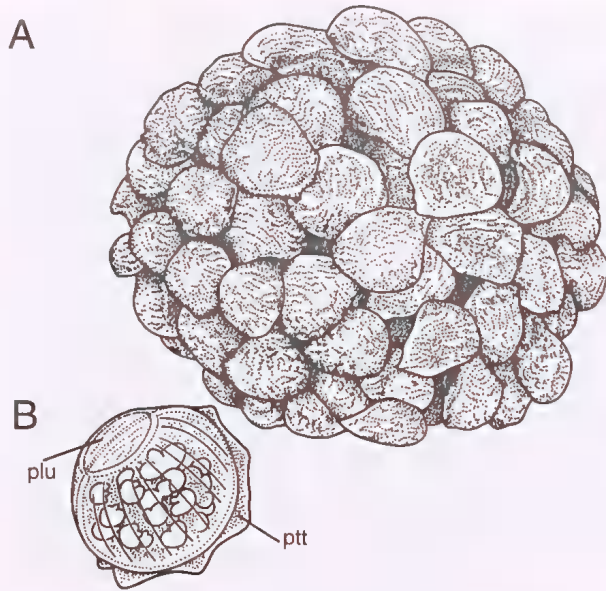


Figure 15.23 The spawn mass and egg capsule of the European neogastropod *Buccinum undatum* (Caenogastropoda, Buccinidae). A, spawn mass of a single individual; B, a single capsule containing young whelks feeding on the central mass of food eggs. The single capsule shows a plug crossed by a suture joining right and left halves of the capsule wall, the product of the bilobed capsule gland, also the peripheral attachment moulded by the foot on to the walls of neighbouring capsules. plu, plug with suture; ptt, peripheral attachment. (After Fretter & Graham 1962) [C. Eadie]

Parthenogenesis

A few freshwater caenogastropods are parthenogenetic, such as the hydrobiid *Potamopyrgus antipodarum* (Boycott 1919), species in the viviparid genus *Campeloma* (Van Cleave & Altringer 1937) and thiarids (Jacob 1957; Stoddart 1983). In some populations, males occur in low numbers, for example *Potamopyrgus* (Patil 1958; Wallace 1978, 1979, 1985), *Campeloma* (van der Schalie 1965) and thiarids (Jacob 1957, 1958; Stoddart 1985).

Gametes

The process of spermatogenesis is summarised by Voltzow (1994). 'Prosobranchs' frequently show sperm dimorphism (see Fig. 1.17). Fertile euspermatozoa (eupyrene or so-called 'typical' sperm) fertilise eggs and are haploid. Nuclear content of infertile paraspermatozoa (so-called 'atypical' sperm) varies: the term oligopyrene is applied when there is less nuclear material than in eusperm, apyrene when nuclear material is absent, and hyperpyrene when there is more nuclear material than in eusperm.

In most patellogastropods and vetigastropods the euspermatozoa have a relatively simple morphology, with a conical acrosome, a short nucleus, a ring of round mitochondria surrounding the centrioles and finally a flagellum (see Fig. 1.17A, B; Franzén 1955, 1970; Koike 1985; Healy 1988a, 1996; Hodgson & Bernard 1988). This type of euspermatozoon is associated with fertilisation within an aquatic medium, either completely outside the animal (ect-aquatic fertilisation) or within the confines of a mantle cavity (ent-aquatic fertilisation) (see Rouse & Jamieson 1987 for definitions). By contrast the euspermatozoa of internally fertilising 'prosobranchs' (some vetigastropods, all Neritopsina – see Fig. 1.17C, Caenogastropoda) have a slender, rod-shaped nucleus (often elongate and partially sheathing the axoneme), an elongate and highly modified mitochondrial sleeve around the axoneme (middle piece), an elongate sleeve of glycogen deposits around the posterior region of the axoneme (glycogen piece) and a short end-piece (axoneme only). Such modifications appear to correlate with a need to swim through viscous fluids of the genital tract and to survive long-term periods of suspended activity in the female duct. Euspermatozoa of internally fertilising taxa are often accompanied by paraspermatozoa whereas those of externally fertilising species are not. Euspermatozoa of several groups have

been investigated ultrastructurally and have proved valuable in resolving taxonomic and phylogenetic problems (Giusti 1971; Healy 1982a, 1983, 1986a, 1986b, 1988a, 1988b, 1993a, 1996; Kohnert & Storch 1984a, 1984b; Koike 1985; Hodgson & Bernard 1988; Hodgson & Foster 1992; Hodgson & Chia 1993).

Nishiwaki (1964) described paraspermatozoa (= dispyrene, apyrene, oligopyrene sperm) from 22 caenogastropods families, based on light microscopic observations, and demonstrated the phenomenon of dimorphic paraspermatozoa in certain species of Viviparidae and Cymatiidae. More recently, ultrastructural studies have provided detailed information concerning the internal morphology and developmental origins of paraspermatozoa, not only within the Caenogastropoda, but also in Neritopsina and certain vetigastropods (see Healy 1988a, 1990a, 1996 and references therein).

Paraspermatozoa differ considerably in size, shape and mobility and have proved to be of considerable taxonomic and phylogenetic importance (Healy 1986a, 1988a, 1988b). In the Cyclophoroidea, Ampullarioidea and Cerithioidea, paraspermatozoa are highly motile and consist of a rod-shaped anterior 'head' region and a posterior cluster of flagella (emergent from the head region) (see Fig. 1.17J–L). In several other caenogastropod superfamilies, the paraspermatozoa are vermiform and show at best only weak movement (Tonnoidea, Cypraeoidea, Muricoidea, Conoidea; see Fig. 1.17M–P) or even lack axonemes altogether (Nishiwaki 1964; Melone, Lora Lamia Donin & Cotelli 1980; Giusti & Selmi 1982a).

In the Janthinoidea (Janthinidae and Epitoniidae, Ankel 1926, 1930; Bülnheim 1962, 1968; Nishiwaki 1964) and Triphoroidea (Triphoridae and Cerithiopsidae, Fretter & Graham 1962; Healy 1990b), the paraspermatozoa are very large, sometimes measuring over 1 mm in length and contain hundreds of internal axonemes which provide motility (see Fig. 1.17Q, R). Clumps of mature euspermatozoa become attached to the posterior 'tail' region of these large paraspermatozoa, thereby forming a motile cellular association known as a spermatozeugma. Such spermatozeugmata appear to fulfil the function of a penis in these aphillic gastropod groups (Graham 1954a).

Other possible functions have been suggested for paraspermatozoa including prevention of premature dispersal of euspermatozoa (in cases of spermatozeugmata formation), nutrition and capacitation of euspermatozoa, possible contribution to oocyte production or capacitation (Hanson, Randell & Bayley 1952; Healy & Jamieson 1981). In internally fertilising taxa, sperm are either transferred by a penis (neritopsines, most caenogastropods) or via a spermatophore (for example, Cerithioidea, Houbbrick 1973, 1988; Vermetoidea, Hadfield 1969; see Robertson 1989 for a review). Both structures are employed in certain taxa (some neritopsines, Bourne 1908; *Littorina angulifera*, Lenderbig 1954; some heteropods, Tesch 1949). The wall of the spermatophore is formed by the testicular epithelium in the vetigastropod *Diodora nubecula* (Medem 1945), but in caenogastropods is a secretion of the pallial genital tract.

Differences in egg size in vetigastropods and patellogastropods relate to size (yolk content) which is correlated with the number of eggs produced and their mode of development. For example the eggs of the European *Haliotis tuberculata* are about 180 µm in diameter, about 10 000 eggs are shed at each spawning, and the seasonal total approximates 23 000 (Pelseneer 1935). These eggs develop to a free larva (Crofts 1937), whereas in *Calliostoma zizyphinum* fewer eggs are produced (260–300 µm in diameter) and development is direct (Crofts 1955; see also review of trochoidean reproductive biology by Hickman 1992).

Many caenogastropods have smaller eggs than vetigastropods and patellogastropods, but compensate by having encapsulated food and/or planktotrophic larvae. Within one family direct or indirect development may occur, direct developers having larger eggs than indirect. In colder waters larval development tends to be suppressed, and is replaced by production of larger eggs.

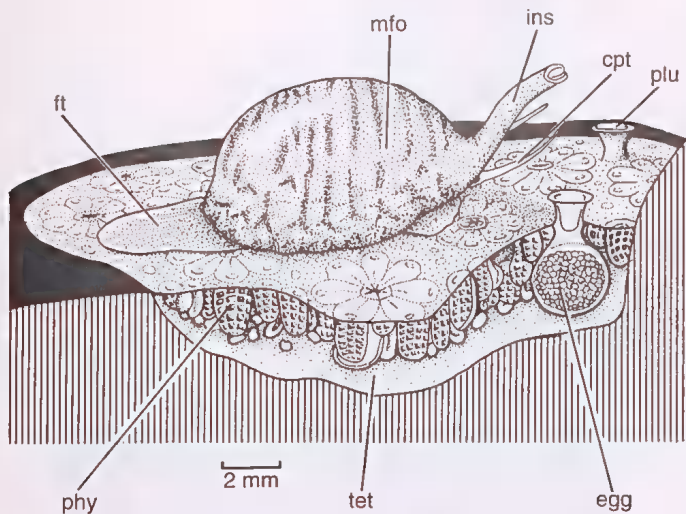


Figure 15.24 The European *Trivia monacha* (Caenogastropoda, Triviidae), crawling over the surface of a colony of the tunicate, *Botryllus schlosseri*, which has been cut vertically in the foreground to show the zooids and an embedded egg capsule. In the right background the neck of a second capsule is visible. Females have a ventral pedal gland, a pit in the middle of the sole, which everts as a papilla and drives the capsule into a cavity in the tunicate test bitten out by the radula. The female then grips the pliable neck of the capsule and moulds it into its final form. cpt, cephalic tentacle; egg, eggs in egg capsule; ft, foot; ins, inhalant siphon; mfo, mantle fold covering shell; phy, pharynx of zooid of tunicate; plu, plug in egg capsule; tet, test of tunicate. (After Fretter & Graham 1962) [B. Scott]

However, direct development is not restricted to large eggs; it also depends on the availability of food eggs. These food eggs, or nurse eggs as they are often called, are arrested in development (Staiger 1950, 1951) and are eaten by developing larvae. Food eggs are produced in, for example, the European rissoid *Rissoa membranacea* (Rehfeldt 1968), and the European buccinids *Colus islandicus* (Thorson 1935), *Neptunea antiqua* (Pearce & Thorson 1967) and *Buccinum undatum* (Fig. 15.23). It has been suggested that production of food eggs represents a parallel to production of typical and atypical sperm (Burger & Thornton 1935).

External fertilisation necessitates synchronisation of spawning and the successful union of gametes. In some species, (for example, *Megathura crenulata* and *Haliotis cracherodi*, Tyler 1939; *Patella vulgata* and *P. caerulea*, Hultin 1948) it is facilitated by pheromones secreted by both gametes, each secreting two. One pheromone produced by the egg accelerates the movement of the sperm and the second, confined to the jelly surrounding the egg (Tyler 1940), agglutinates the sperm when it reaches the egg, but has no effect on sperm of other species (Tyler & Fox 1940). One pheromone secreted by the sperm slows their movement before liberation, and the second, in the sperm head, causes local solution of the jelly membrane in *Patella vulgata* and *P. caerulea* (Hultin 1948). It has been suggested that the acrosome carries a lysin that destroys the membrane (Dan & Wada 1955).

Little work has been done on sex determination. Our present knowledge suggests that male 'prosobranchs' are heterogametic and females are homogametic, that is, the sex chromosomes of males are dissimilar and those of females are similar (Burch 1960; Patterson 1963, 1965).

Spawn

The great diversity of spawn in caenogastropods relates to the number of eggs in a spawn mass, whether they share a communal store of albumen, the composition of the membranes surrounding the albumen, the moulding of these by the pallial duct and foot, the method of deposition, and the strengthening of the outer wall by inorganic particles. Some marine species lay their eggs in long

gelatinous strings compacted into coils by movements of the snail, aided by the foot, as in strombids (Robertson 1959) and cerithiids (Houbrick 1973). Each egg is embedded in albumen and the eggs are bound together in another secretion from the pallial duct, providing a tacky external surface which adheres to the substratum. *Strombus raninus* produces a spawn mass about 20 m long, with an estimated 400 000 to 460 000 eggs (Robertson 1959), whereas the small snail *Cerithium muscarum* (about 20 mm in length) produces a spawn mass with an estimated 52 000 eggs (Houbrick 1973). Some littorinids also have gelatinous egg masses, but of smaller size and containing fewer eggs (Fig. 15.26C; Hertling 1928; Lebour 1937; Thorson 1946; Anderson, H. 1958; Sacchi & Rastelli 1966; Smith, D.A.S. 1973; Heller 1975; Grahame 1977; Goodwin 1979; Hannaford Ellis 1979; Fretter & Graham 1980; Reid 1988, 1989a). Planktonic capsules are typical of many intertidal littorinids (Bandel 1974a; Mileikovsky 1975; Reid 1986b, 1989a; Buckland-Nicks & Chia 1990) and many species produce only one egg per capsule. The final form of a spawn mass of a littorinid, particularly when it is planktonic, is determined by the ovipositor, from which it is liberated to the plankton or passed along a temporary groove to the foot to be pressed onto the substratum.

The thickness and texture of the wall of caenogastropod egg capsules is correlated with the mode of incubation or with the development of the young. It is thin in capsules deposited in the living tissues of colonial animals on which the adult browses: sponges (*Cerithiopsis*, Lebour 1933a), or compound ascidians (Fig. 15.24) (*Trivia*, Pelseneer 1926; *Lamellaria*, Ankel 1935; *Velutina*, Diehl 1956; *Austromitra*, Ponder 1972a); also in those species that brood over their capsules (Fig. 15.28) or retain them in a brood chamber (Fig. 15.25). The walls of exposed capsules (Fig. 15.111G) may be strengthened by incorporating mud or sand particles in the surface layers, as in some hydrobiids, naticids (Giglioli 1955; Ziegelmeier 1961) and epitioidids (Vestergaard 1935). Alternatively, the strengthening may be due to secretions produced by the pallial oviduct as in most neogastropods, among them muricids (Ankel 1937; Fretter 1941; Bayne 1968), buccinids (West 1979), olivids (Marcus, Ev. & Marcus, Er. 1959a), and cones (Kohn 1961). These capsules have varying shapes, a plugged apex from which the young escape (Fig. 15.23B), and a basal flange for attachment (Thorson 1935, 1940, 1946; Lebour 1937; Knudsen 1950; Kohn 1961; Marcus, Er. & Marcus, Ev. 1962; Ponder 1973a; Bandel 1974b; D'Asaro 1988, 1991, 1993). Some must withstand a long period of embryonic development, even up to seven months in *Nucella lapillus* living in

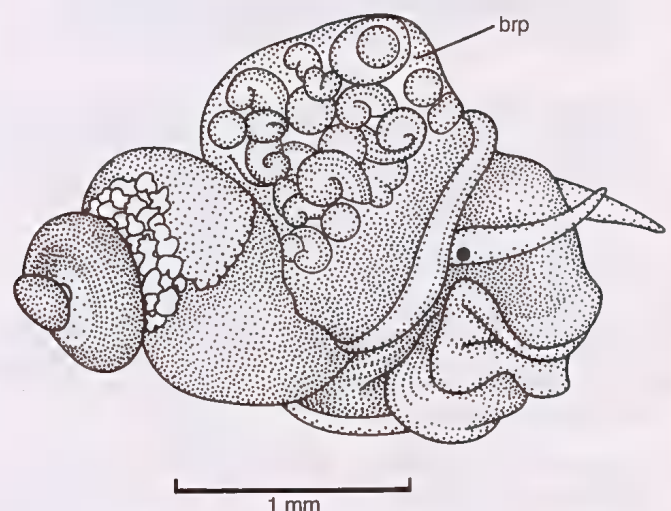


Figure 15.25 The New Zealand caenogastropod *Potamopyrgus antipodarum* (Hydrobiidae) lives in brackish and fresh water and is a successful colonising species which has been introduced to Australia. The shell has been removed to show the unfertilised eggs which develop to young snails, in the brood pouch formed from the distal pallial oviduct. brp, brood pouch. (After Thorson 1946) [C. Eadie]

15. PROSOBRANCHS

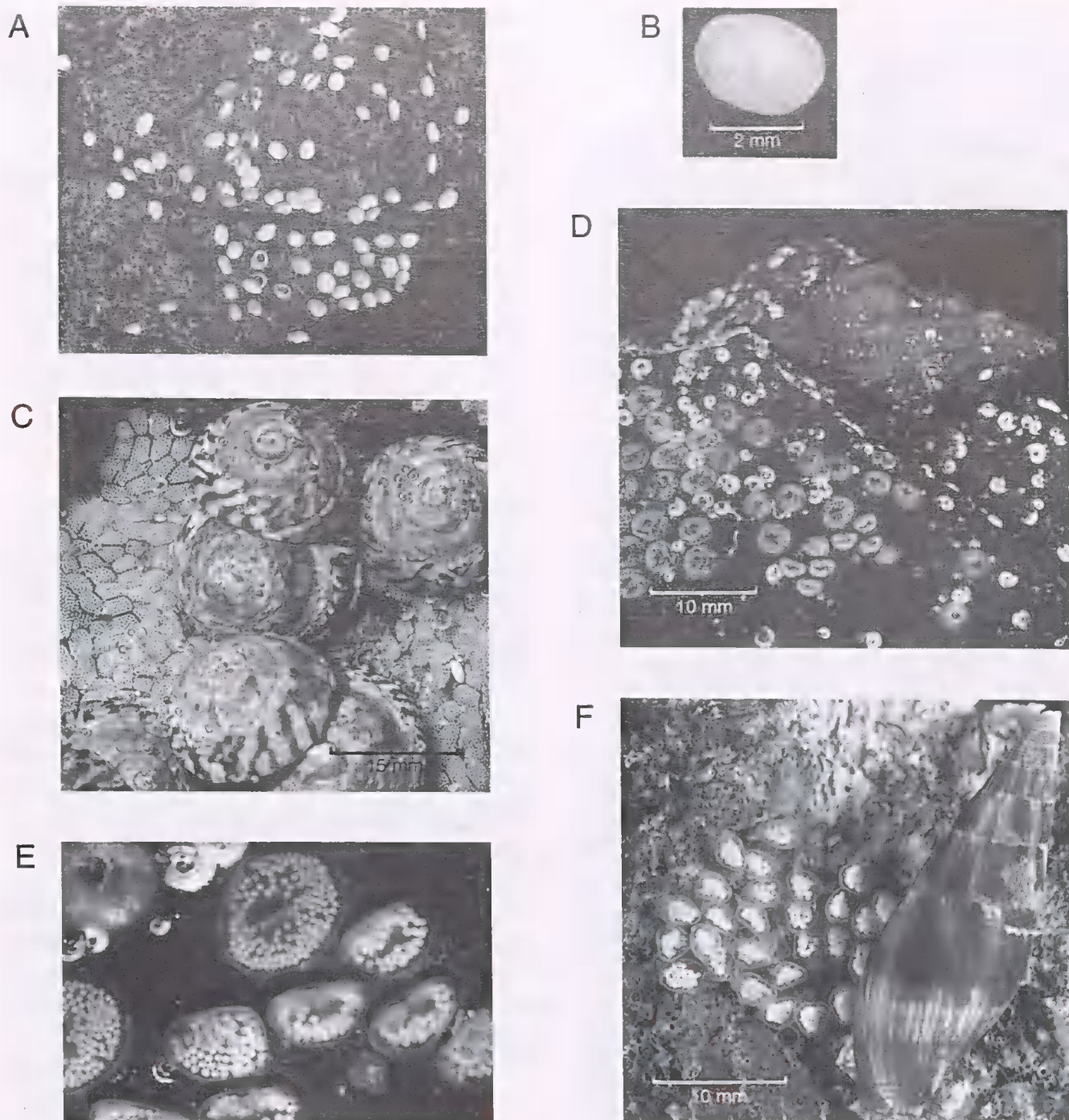


Figure 15.26. Prosobranch egg masses. **A, B,** *Nerita atramentosa* (Neritopsina, Neritidae): **A,** white egg masses laid on rock in intertidal pool; **B,** detail of one egg mass. **C,** *Bembicium nanum* (Caenogastropoda, Littorinidae), an aggregation of egg-laying snails in a high tidal pool. **D, E,** *Cronia contracta* (Caenogastropoda, Muricidae): **D,** snail and egg masses on underside of rock; **E,** detail of egg masses showing those recently laid with many tiny eggs (seen through the transparent egg capsule) and older ones with a few large juveniles about to hatch (having eaten the nurse eggs). **F,** *Mitra cooki* (Caenogastropoda, Mitridae), laying eggs.

[W.B. Rudman]

the White Sea (Matveeva 1955). The capsule wall is made of protein fibres reinforcing a matrix of polysaccharide and the innermost part of the wall contains tyrosine (see Fretter & Graham 1994 for more details). Animals living on soft substrata often use their own shells or those of others to obtain a sufficiently firm base of attachment for their capsules.

The production of egg capsules probably evolved independently in neritopsines (Fig. 15.26A, B) and caenogastropods. Neritids add particles from the crystal (or reinforcement) sac at the posterior end of the oviduct (Andrews, E.A. 1935; Fretter 1946). Typically, in caenogastropods the capsule is moulded by the foot which also fixes capsules to the substratum (Fig. 15.26C–E). Many Cerithioidea have ovipositors on the right side of the foot, which have become internal in the foot in Diastomatidae (Houbrick 1981c) or associated with brood pouches in some

groups (see below). In some neotaenioglossans, such as species of *Trivia*, *Lamellaria* and *Charonia*, and many neogastropods, often with large, elaborate capsules, females have a ventral pedal gland appearing as a pit projecting into the pedal musculature and opening on the sole (Ankel 1929; Fretter 1941, 1946; Franc 1943; Fretter & Graham 1962; Ponder 1973a). The capsule is transferred to the pedal gland from the oviduct and is moulded within it, its secretions helping to harden the wall before deposition.

Those neritopsines and caenogastropods that have colonised freshwater or land generally produce small numbers of eggs, often only one per capsule. They have an enlarged supply of yolk or additional food and water in the form of albumen, as in the terrestrial European littorinioidean *Pomatias* (Fig. 15.27A), and occasionally, food eggs, as in some neritids (Fretter & Graham 1962).

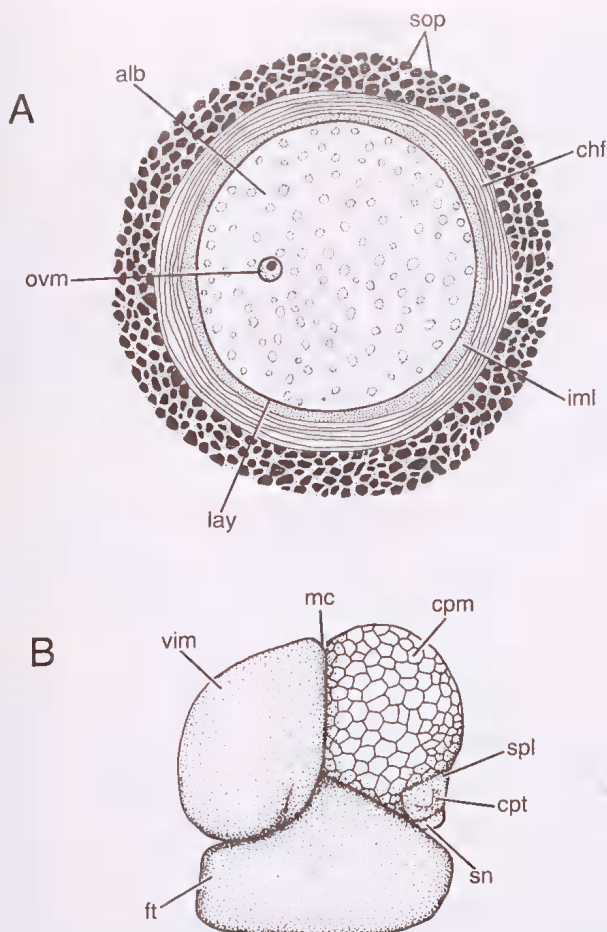


Figure 15.27 The eggs and early larva of the European terrestrial littorinoidean *Pomatias elegans* (Caenogastropoda, Pomatiidae): A, section of egg capsule; B, embryo at 42 days after torsion, seen from the right. alb, albumen; chf, fibres of conchiolin in mucus; cpm, cephalic mass; cpt, cephalic tentacle; ft, foot; iml, inner mucous layer; lay, deeply staining layer around albumen; mc, mantle cavity; ovm, ovum; sn, snout; sop, soil particles; spl, sense plate; vim, visceral mass. (After Creek 1951) [B. Scott]

Flooding or water loss is reduced by a thick egg covering, a calcareous shell (*Pila*, Bahl 1928), or a layer of adherent soil. In some freshwater species protection for the embryo is provided by ovoviviparity (*Viviparus*, *Potamopyrgus*; Fig. 15.25), and in some terrestrial species there may be a large cephalic vesicle (Fig. 15.27B) which absorbs the ample supply of albumen while the capsule wall takes up soil water and salts (*Pomatias elegans*, Creek 1951; cyclophorids, Kasinathan 1975).

Brooding and Parental Care

A few species exhibit varying degrees of parental care. In the vetigastropod *Clanculus bertheloti* (Trochidae) for example, eggs embedded in mucus are carried by both sexes in the spiral grooves of the shell (Thorson 1967) and in another trochid, *Margarites vorticiferus*, the female carries them in the umbilical region (Lindberg & Dobbertein 1981). Alternatively, eggs may be retained in the mantle cavity as in a few patellogastropods, such as *Proclacmaea* (Thorson 1935) and *Rhodopetala* (Golikov & Kussakin 1972). Some caenogastropods brood egg capsules held by the foot beneath the shell – calyptreids, *Capulus* (Fig. 15.28), hipponicids (Fig. 15.123; Yonge 1960a; Laws 1970; Knudsen 1991) and cypraeids. Others retain capsules in the mantle cavity. Examples are some species of the mangrove littorinid genus *Littoraria* (Lenderbig 1954; Struhsaker 1966; Reid 1986b); all coralliophilines (see Wells & Lalli 1977); and the vermetid genus *Petalocochus*, and the siliquariid *Stephopoma* (Morton, J.E. 1951b, 1951c, 1951d). Some modified eulimids retain eggs in the pseudopallial cavity (Ivanov 1945; Mandahl-Barth 1946). In others, capsules are attached to the inner surface of the shell (vermetids, Morton, J.E. 1951b, 1951c, 1951d), to the umbilical region (for example, in some trochids) or to a buoyancy float secreted by the foot (Janthinidae, Laursen 1953).

Fertilised eggs provided with albumen may be retained in the anterior part of the pallial oviduct, which acts as a brood pouch (*Viviparidae*, Cyclophoridae, Tielecke 1940; *Melanoides torulosa*, Seshaiya 1940; *Potamopyrgus antipodarum*, Fig. 15.25; Fretter & Graham 1962; *Littorina saxatilis*, Fretter & Graham 1980; *Janthina janthina*, Graham 1954a; *Polygireulima*, Warén 1983a), or in a special pouch formed by an invagination of the body wall at the side of an ovipositor and passing deeply into the tissues of the head (see Fig. 1.19B; some Thiaridae, Moore 1899; Starmühlner 1969; *Pyxipoma*, Morton, J.E. 1951c; Planaxidae, Risbec 1935; Thorson 1940; Houbrick 1987a). Normally, development is completed in brood pouches, however, in *Melanoides* species (Thiaridae), and most populations of *Planaxis sulcatus* (Houbrick 1987a), *Polygireulima* and *Janthina* species, the young hatch as veligers.

Development and Larvae

Indirect development (but not planktotrophy) is probably the primitive state for Gastropoda (Chaffe & Lindberg 1986; Haszprunar 1988a; Haszprunar, Salvini-Plawen & Reiger 1995), though commonly, even amongst members of one genus the larval stage may be suppressed. Patellogastropod and vetigastropod trochophore larvae hatch from their individual eggs into the plankton a few hours to a few days after fertilisation. During their brief planktonic life little or no external food is taken. The swimming stage is followed by a longer swimming-crawling stage when activity is hampered by the completion of torsion.

Caenogastropods complete torsion before hatching as a veliger (Fig. 15.29). The larvae feed more or less continuously, rising through the water, aided by their large, bilobed velum and with their foot uppermost to gather food particles, then withdrawing the velum and sinking, only to rise again (Fretter & Montgomery 1968). Considerable vertical migration may be exhibited by larvae of species living at great depths, such as the rissoid *Benthonella tenuis* at 2000–4000 m (Bouchet 1976) in the Atlantic. Differential horizontal movements of layers of the water column may break the vertical alignment of the larvae and sweep some beyond the limits of the area of origin. The veligers continue to feed and grow and under suitable conditions may settle. This mechanism on a large scale may have played an important part in the wide distribution of some caenogastropods, especially tonnoideans such as the ranellid *Septa parthenopaum*, as well as various cassids, tonnids and bursids (Scheltema 1966, 1972a; Scheltema & Williams 1983); some of these long-distance, long-lived, or teleplanic, larvae are capable of surviving for several months in the plankton.

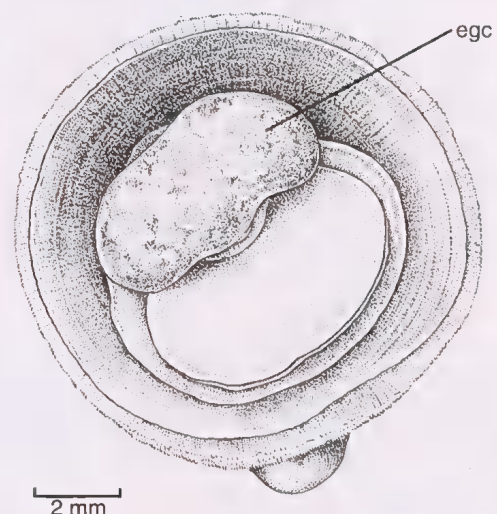


Figure 15.28 A female of the European caenogastropod *Capulus ungaricus* (Capulidae), ventral view, showing the brooded egg capsules. egc, egg capsules. [P. Winther]

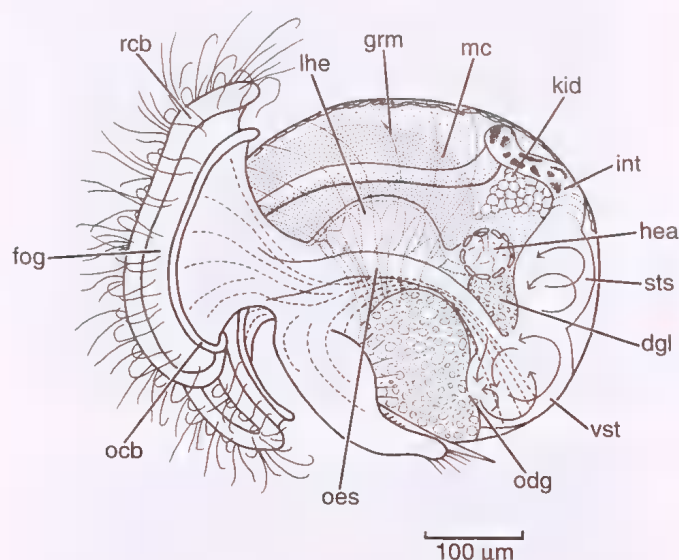


Figure 15.29 Veliger larva of the European neogastropod *Nassarius reticulatus* (Caenogastropoda, Nassariidae), left view, showing the course of the gut. Arrows indicate the action of cilia on food in the stomach. The retractor muscle passing to the velum and foot is shown by broken lines. dgl, digestive gland; fog, food groove; grm, growth line on shell; hea, definitive heart; int, intestine; kid, kidney; lhe, larval heart; mc, mantle cavity; ocb, cells bearing postoral ciliary band; odg, opening of digestive gland to stomach; oes, oesophagus; rcb, cells bearing preoral ciliary band; sts, style sac; vst, ventral (digestive) chamber of stomach. (After Fretter & Pilkington 1971) [B. Scott]

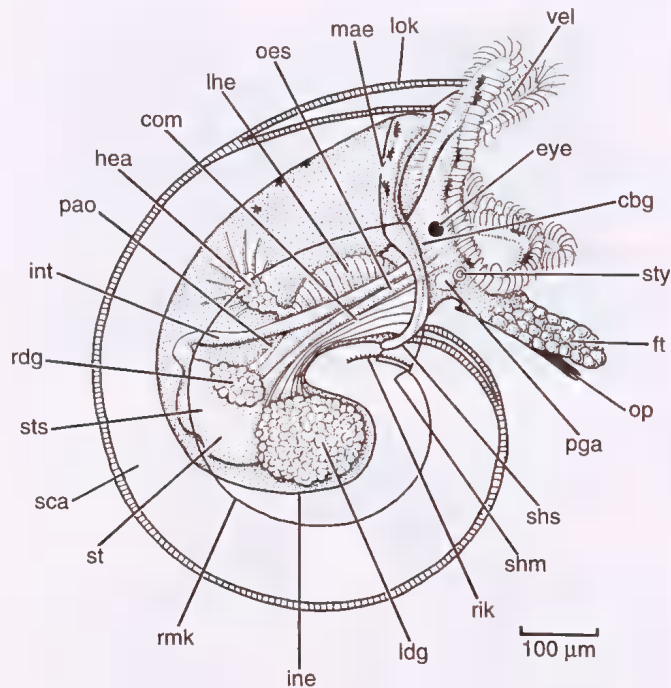


Figure 15.30 Echinospira larva of the European caenogastropod *Lamellaria perspicua* (Velutinidae), right view. The velum is not fully expanded. cbg, cerebral ganglion; com, columellar muscle; eye, eye; ft, foot; hea, developing definitive heart; ine, inner part of echinospira shell; int, intestine; ldg, left lobe of digestive gland; lhe, larval heart; lok, left outer keel of shell; mae, mantle edge; oes, oesophagus; op, operculum; pao, posterior aorta; pga, pedal ganglion; rdg, right lobe of digestive gland; rik, right inner keel of shell; rmk, right middle keel of shell; sca, space between outer (scaphoconch) and inner parts of shell; shm, point where inner and outer shells meet when larva is fully extended; shs, chiselled surface of shell; st, stomach; sts, style sac region of stomach; sty, statocyst; vel, velum. (After Fretter & Graham 1962) [B. Scott]

Veligers of some caenogastropods in the families Lamellariidae, Eratoidae and Capulidae (Lebour 1931, 1935, 1937) have a large velum and an elaborate shell which helps to keep them afloat (Fig. 15.30). In this echinospira larva, the innermost part of the shell – a layer of conchiolin reinforced with calcareous matter – is closely applied to the mantle and, except around the aperture, is separated by a fluid-filled space from a considerably larger outer layer composed of conchiolin. The fluid between the two shell layers is initially extrapallial (in other molluscs it occurs between the tissues and the shell). As the larva grows and the velum enlarges its withdrawal is hampered by the restricted shell opening. This opening is enlarged ventrally by the chiselling of the ventral edge of the operculum, an action which opens the space between the two shell layers and allows the external medium to enter. At metamorphosis the outer shell or scaphoconch is lost (Fretter & Graham 1962).

During the life of the caenogastropod veliger structural changes related to adult life occur, those associated with feeding are most evident. The odontophore develops beneath the larval gut, ready to be brought into action at metamorphosis, when it passes through the nerve ring and protrudes from the buccal floor. In neogastropods (*Nassarius*, *Mangelia*, Fretter 1972), the proboscis, together with the definitive anterior oesophagus, develops in a similar position. The late veliger is a swimming-crawling stage searching for a suitable substratum on which to settle; it responds negatively when the substratum is inappropriate. Chemotactic and thigmotactic stimuli initiate settlement, which may be induced by organic properties of the substratum beneficial to the adult (Kiseleva 1967; Struhsaker & Costlow 1968; Fretter & Manly 1977a, 1977b). Metamorphosis, often involving a number of changes occurring simultaneously, must be speedy. Secretion from the foot anchors the body (Fretter & Manly 1977b) and the velum is lost in some species (Scheltema 1956; Fretter 1972), or swallowed and digested in others (Fretter 1969, 1972). In limpet-like forms, the operculum is usually lost, and changes in the pedal musculature prevent the snail from withdrawing into the coil of the shell, the aperture of which is pressed against the substratum.

Planktotrophy has evolved independently in at least two gastropod groups – Neritopsina (Bandel 1982) and Apogastropoda (Caenogastropoda and Heterobranchia). It may have evolved independently in the two members of the Apogastropoda (Ponder 1991a; Ponder & Lindberg 1997).

Direct development is only possible with internal fertilisation and is often accompanied by the development of secondary protection for the eggs such as capsules or jelly, or a brood chamber. It occurs in many caenogastropods groups in particular (see Thorson 1946, 1950; Fioroni 1982).

The Protoconch

The protoconch or larval shell is produced during larval or intracapsular life. In planktotrophic 'prosobranch' gastropods (Neritopsina, Caenogastropoda) two parts to the larval shell can usually be distinguished, protoconch I and II. Protoconch I is formed in the capsule. Protoconch II, the distinct secondary larval shell, develops while the larvae is feeding in the plankton. Therefore, the presence of a second protoconch can be taken as an indicator of a planktotrophic stage in a life cycle (Bandel 1982).

Bandel (1982, 1986) argued that the apparent coiling of the vetigastropod protoconch is the result of physical deformation of the non-mineralised shell, followed by calcification, and not the result of differential growth. The surface of the protoconch is smooth or variously sculptured, usually differently from the sculpture of the teleoconch. The morphology of the protoconch is often used as an important character in classification.

Subclass EOGASTROPODA

This group was introduced recently by Ponder & Lindberg (1996) to encompass the Patellogastropoda (reviewed by Lindberg 1988a) together with its ancestors, which were probably sinistrally coiled (Lindberg 1981a, 1988a), and perhaps included members of the Palaeozoic Paragastropoda (Linsley & Kier 1984). The Patellogastropoda may be a relatively late offshoot from this group, the first patellogastropod fossil being from the Middle Ordovician (Yochelson 1988) whereas possible coiled ancestral forms appeared in the Lower Cambrian.

The patellogastropod radula, and presumably the radula of all eogastropods, is unique in its function (Ankel 1936a; Fretter & Graham 1962), being stereoglossate (Salvini-Plawen 1988). It is now clear that the group, including patellogastropods is the sister taxon to the orthogastropods (Fleure 1904; Golikov & Starobogatov 1975; Shileyko 1977; Graham 1985; Haszprunar 1988a, 1988b; Lindberg 1988a); the Patellogastropoda is no longer considered to be a specialised branch of the 'Archaeogastropoda'.

The anatomical and other peculiarities of the extant members of this group are discussed under Patellogastropoda.

Order PATELLOGASTROPODA

The Patellogastropoda is the most primitive group of living gastropod molluscs (Golikov & Starobogatov 1975; Graham 1985; Wingstrand 1985; Haszprunar 1988a; Lindberg 1988b), and is the sister taxon of all other gastropods (Ponder & Lindberg 1996, 1997). Members of this taxon are characterised by secondarily flattened shells, two pairs of outer lateral teeth, subpallial sensory streaks, a labral commissure, shell microstructures including foliated and cone crossed-lamellar layers, the presence of pallial gills, rotation of the pericardium, the presence of 'Spengel's' or 'wart' organs, a rectum that passes outside the pericardium, and the loss of the style and gastric shield (see Table 15.2). Many of the other characters that set patellogastropods apart from other gastropods are primitive or plesiomorphic characters that they share with taxa such as the Polyplacophora (chitons) and Monoplacophora. These include the radular morphology and musculature, lateral teeth with ferrous oxides, the presence of a subradular organ (licker) and statocyst position. Although an operculum and epipodial tentacles are absent in the adult snail, they are present in the veliger (Smith 1935; Anderson 1966).

Traditionally the Patellogastropoda have been divided into three major groupings: the Patellidae, Nacellidae and Lottiidae (the latter previously referred to as the Acmaeidae). These groupings are characterised by gill and radular features. All three groups are found in Australia. A phylogenetically based classification places the Patelloidea as the most primitive taxon (Fig. 15.31; Table 15.2). From this perspective, the evolutionary trend in the Patellogastropoda is predominantly to reductions and simplifications of character states (Lindberg 1988b). Often the character trends appear to be paedomorphic (Gould 1977), and suggest progenesis or post-displacement as processes, rather than neoteny (Alberch, Gould, Oster & Wake 1979). Some of these trends also parallel evolutionary trends in other 'prosobranch' taxa. Paedomorphic trends include reduction in shell size, in the number of radular teeth, in the complexity of gut looping patterns, in the age of first reproduction, and in the complexity of respiratory structures (Lindberg 1988b). New and bizarre anatomies also occur, apparently the result of releases from the constraints of adult morphology (Gould 1977) (for example, the heart morphologies of the brooding lottiids, Lindberg 1983, 1988b, 1988b). The trends are independent in different organ systems and structures and not global features – the organism is always a mosaic of heterochronic process.

The classification used here and in Table 15.2 corresponds to the phylogenetic hypothesis presented in Figure 15.31. Names are applied only to clades (monophyletic groups). Redundant names are not used. For example, taxa included within the diagnoses of Patellina and Patelloidea are identical, and therefore only the

name Patelloidea is used. The ranks adopted here have been determined by the suffixes of taxon names currently in general use, and are presented only to provide internal consistency with the other contributions in this work.

Most early workers [Cuvier 1817–1829; Gray 1857; Troschel (& Thiele) 1856–1893; Dall 1871a, 1871b; Pilsbry 1891; Theim 1917] distinguished the Patellogastropoda at the ordinal level. However, Thiele (1925b) reversed this practice and placed the group as a suborder within the Archaeogastropoda, where they remained for the next 50 years. Golikov & Starobogatov (1975) removed the patellacean limpets from the Archaeogastropoda and returned them to the order Docoglossa in the subclass Cyclobranchia. Since Golikov & Starobogatov proposed the removal of patellaceans from the Archaeogastropoda, the accumulation of new data as well as the re-examination of data from earlier studies has without exception supported their action. Lindberg (1986a) proposed the order Patellogastropoda for the families Patellidae, Acmaeidae and Lepetidae, rejecting the name Docoglossa because it applies to a level of organisation (or grade) of radular morphology, musculature and function that is not restricted to the clade Patellogastropoda. The docoglossate condition also occurs in the Monoplacophora and Polyplacophora (Ankel 1938; Lemche & Wingstrand 1959; Golikov & Starobogatov 1975; Lindberg 1985; Wingstrand 1985).

Australian patellogastropods were first monographed by Oliver (1926) who treated the acmaeoid fauna in a review of the Australasian region. Oliver's treatment incorporated the earlier work of Iredale (1915, 1924) and associated radular characters with the shell characters originally used by Iredale and other workers for New Zealand and Australian genera. By studying the radulae, Oliver made the important observation that shell and radular characters were not always in agreement. He also proposed a biogeographical and evolutionary history for the group in the Pacific basin, and proposed five new genera for Australian species: *Chiazacmea*, *Asteracmea*, *Actinoleuca*, *Conacmea* and *Subacmea*.

Macpherson (1955) was the first to treat both patelloidean and acmaeoid taxa in the same systematic revision. Macpherson, like Oliver, incorporated radular characters into her descriptions and provided comprehensive species synonymies. Macpherson also presented detailed habitat information for each species. Although her treatment of patelloidean taxa is adequate, several *Patelloidea* species and all the small *Asteracmea* species were omitted.

Ponder & Creese (1980) treated the acmaeoid genera *Notoacmea*, *Collisella*, and *Patelloidea* in the most recent revision. Once again, shell and radular characters were used to diagnose genera and species; the genus *Asteracmea* was not treated because of a lack of material. Ponder & Creese were able to resolve several especially knotty nomenclatural problems including the identities of *Notoacmea flammea*, *Patelloidea insignis* and *Collisella mixta*.

In addition to these larger revisions, smaller regional checklists and studies include Hedley's (1916) index of Western Australian molluscs, May's (1923) index of Tasmanian shells, Cotton's (1959a) treatment of the South Australia species, Iredale & McMichael's (1962) listing for New South Wales and Macpherson & Gabriel's (1962) for Victoria. The Australian patellogastropod species have also been treated in worldwide monographs by Powell (1973) and Christiaens (1973) for the Patellidae, and Christiaens (1975a, 1975b, 1976) for the Acmaeidae (= Acmaeoidae).

Although the species-level nomenclature for most members of the Australian patellogastropod fauna now appears to be relatively stable, the groupings of higher level taxa, and especially their evolutionary histories, are still unclear. The presence of members of the Patelloidea, Nacellidae, and Lottiidae in the Australian fauna has been recognised since the earliest biological explorations of the region (for example, Quoy & Gaimard 1830–1834); however, members of other higher patellogastropod taxa have only been found in the region in the last 10 years. For example, Marshall (1985) reported the first occurrence of the deep-water patellogastropod taxon Pectinodinae (Acmaeidae) off

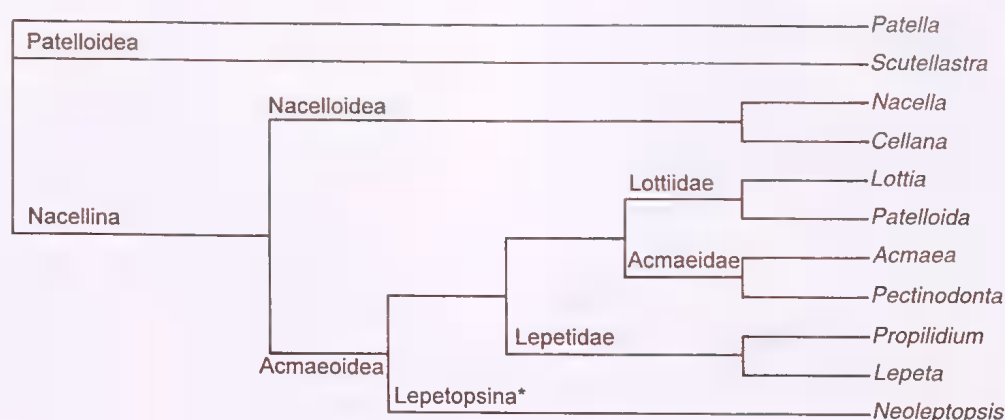


Figure 15.31 Hypothesised relationships amongst the Patellogastropoda. The unrooted tree represents the single most parsimonious tree based on 45 shell, external and internal anatomical characters for 12 representative genera. Taxon names refer to clades discussed in the text, with the exception of Patelloidea which is paraphyletic. Tree length = 75 steps; consistency index = 0.827; retention index = 0.841. *For discussion of status see text.

of New South Wales and in a second paper (Marshall 1986), transferred *Acmaea parva* var. *tasmanica* from the Cocculinidae to the Propilidiinae (Lepetidae). The diversity of higher patellogastropod taxa in the Australian fauna equals or exceeds other biogeographical regions.

The recognition and perception of characters used to distinguish taxa in the Patellogastropoda has substantially changed since Linnaeus (1758) diagnosed the group as one of the original molluscan genera, including in it all limpet-like gastropods. With the exception of shell microstructure, most diagnostic features of the Patellogastropoda relate to aspects of the animals' anatomy, and in particular the alimentary (radula, jaws, gut), respiratory (gills), and reno-vascular systems.

Although Haszprunar (1988a) has argued that the limpet morphology of patellogastropods is primitive rather than derived, a coiled ancestor is suggested by multiple lines of evidence including outgroup arguments [either cyclomyan (coiled) Monoplacophora (Peel 1980; Harper & Rollins 1982; Runnegar 1983; Runnegar & Pojeta 1985) or Cephalopoda (Lauterbach 1983; Ponder & Lindberg 1997)], comparative larval development (Bandel 1982), the presence of asymmetric protoconch growth (Morse 1910; Thompson 1912; Smith 1935; Lindberg 1981a), and the presence of an operculum in early ontogeny (Lindberg 1981a; Stanley 1982). The coiled sister taxon of the Patellogastropoda has yet to be discovered, but was undoubtedly present in the early Palaeozoic (approximately 500 mya). One possible member of the sister taxon is the extinct family Platyceratidae which shares shell features with patellogastropods (Carter & Hall 1990). Both coiled and limpet-like taxa would probably share the primitive stereoglossate condition of the radula (Ankel 1938) and the presence of ferrous oxides in the radular dentition.

The diversity of shell microstructure in the Patellogastropoda exceeds that for all other gastropods combined. Thus, shell structure characters are especially useful diagnostically; they can often be obtained for fossil taxa as well (Theim 1917; MacClintock 1967; Lindberg 1988a; Carter & Hall 1990; Hedegaard 1990). The shells of these limpets are composed of between four and six layers, including the myostracum (see Fig. 15.32). These shell layers differ in crystal structure, thickness, and sometimes colour. They appear in the interior of the patellogastropod shell as concentric bands of different colours, lustres and textures. These bands delimit the interior surface of the shell and have been described by terms such as shell margin, intermediate area, muscle scar, central area and spatula. In the Patelloidea, the exterior of the shell is foliated; a thin veneer of homogeneous layer may be present in some taxa. Crossed-lamellar layers are also present

above the myostracum. Different patelloidean taxa have differentially emphasised either the crossed-lamellar (*Scutellastra*) or foliated layers (Patellidae). The Patellidae can also have a secondary secretion of foliated material within the myostracum. Within the Nacelloidea, foliated structures dominate and when present, crossed-lamellar structures above the myostracum are thin layers. Foliated structures are also prominent in the Lepetopsina (McLean 1990). Within the remaining Acmaeidea taxa, crossed lamellar structures are more prominent than foliated ones, and the foliated layers are completely absent in the Lottiidae. Crossed-lamellar structures within the Patellogastropoda include commarginal crossed-lamellar, complex crossed-lamellar, and irregular crossed-lamellar structures.

The external anatomical features of some patellogastropod taxa are shown in Figure 15.33. The head bears a pair of cephalic tentacles dorsally, typically with a eye at the base of each (Fig. 15.33B, D). The mouth opens ventrally on the head and is surrounded by a fine fringe of epidermis. In some species, a pair of oral lappets is present on each side of the mouth (Fig. 15.33E). The foot is large and oval, filling the aperture of the shell. The head and the sides of the foot are pigmented in some species.

The mantle is continuous around the perimeter of the shell aperture and extends over the head area and posteriorly to cover the viscera (Fig. 15.33A). The mantle secretes the shell, serves as an auxiliary respiratory surface (especially the surfaces above the head region) and is important in sensory reception. The mantle margin around the aperture is divided into two areas: an outer glandular zone which is active in shell secretion, and an inner branchial zone which is involved in respiration. The ventral surface of the branchial zone may be developed into a series of lappets or swellings (commonly referred to as the pallial gill, branchial cordon or secondary gill; Fig. 15.33A, B), or it may be smooth (Fig. 15.33E, F). The outer edge of the mantle is lined with a single row of retractable sensory tentacles (Fig. 15.33A) which contain photoreceptors, tactile receptors and chemoreceptors. In the Patelloidea and Nacellidae, mantle tentacles and their bases are often pigmented complexes.

Patellogastropods may have a single left ctenidium over the head (Fig. 15.33C, D), and/or a pallial gill (Fig. 15.33A, B), or lack specialised respiratory structures completely (Fig. 15.33E, F). Gill characters were the first anatomical features used in the taxonomy of the Patellogastropoda. Historically, they have been considered as the most conservative characters in patellogastropod systematics, and therefore the most reliable for taxonomy (Eschscholtz 1833; Gray 1833; Dall 1871b; Pilsbry 1891;

Grant 1937; Powell 1973). This assumption has been so pervasive that taxa and phylogenies suggested by other anatomical characters have been ignored, or their acceptance has been made conditional on their concurrence with gill characters. More recent work has raised serious doubts about how conservative gill morphologies really are in the Patellogastropoda (Lindberg 1981b, 1988a; Lindberg & McLean 1981; Hickman & Lindberg 1985; Lindberg & Squires 1990). For example, a particular character state such as presence of pallial gills, can be found in all members of a taxon (Patelloidea) or can be unique to a single species within a subclade (*Lottia gigantea*). This does not mean that gill characters are useless for determining relationships; it only means that the uniqueness of their distribution cannot be assumed, but must be examined in the context of all characters.

The alimentary system begins at a ventral mouth which opens into the buccal cavity containing the jaw and the radula. Continuous with the buccal cavity are the pharynx and oesophagus. The oesophagus turns to the right in the midvisceral region and opens into the fore stomach, which is located slightly to the right of centre in the visceral mass. Upon leaving the stomach and before the rectum, the hindgut typically makes numerous loops.

Many characters used in previous classifications have come from the alimentary system, the most widely used ones from the radula (Fig. 15.34). Since Dall (1871b) proposed the first taxa based

solely on radular characters, many workers, including Iredale (1915), Oliver (1926), Grant (1937), Koch (1949), Fritchman (1960), McLean (1966), Moskalev (1970), Powell (1973), Christiaens (1975a, 1975b), Ponder & Creese (1980) and Lindberg (1981c), have used radular characters to define and infer relationships among taxa. Most workers have used number of teeth, tooth shape, and tooth size to define groups. Although radular morphology is diagnostic at the specific level, it must be used with care when inferring relationships because there is marked convergence in the radulae of taxa that belong to different clades, but occupy similar adaptive zones (McLean 1966; Lindberg & McLean 1981; Lindberg 1983; 1988a). Classifying taxa solely on radular characters often forces one to assume extensive convergence in shell structure, arrangement of respiratory structures and arrangement of the alimentary canal, even though these systems may give concordant phylogenies.

Tooth number is a more conservative radular character than tooth morphology, but its value is complicated by fusion of teeth, loss of tooth fields, and by use of different methods of counting teeth and cusps (Lindberg & McLean 1981). There is a decrease in the number of lateral teeth and uncini in the Patellogastropoda and a trend to increasing complexity in basal plate morphology from Patelloidea (Fig. 15.34A) to Nacelloidea (Fig. 15.34C) to Acmaeidea (Fig. 15.34G) (basal tooth plates are thickened pads

Table 15.2 Unranked classification of the Patellogastropoda and apomorphies supporting the relationships illustrated in Figure 15.31.

Taxon	Apomorphies
Patellogastropoda	Shell secondarily flattened; 'Spengel's' or wart organs present; shell microstructure foliated; two pairs of outer lateral teeth; chromosomes 2n = 9; subpallial sensory streaks present; labral commissure present; pallial gills present; pericardium rotated; rectum passing outside pericardium; style and gastric shield lost.
Patellina (=Patelloidea)	One pair of salivary glands each with two pairs of ducts; oesophagus rotated >230°; outer shell layer foliated; five pairs of radular cartilages.
Scutellastra	Crossed-lamellar shell layers dominant; acrosome simple.
Patellidae	Foliated shell microstructures predominant; innermost shell layer foliated; inverted-V radular tooth configuration in <i>Cymbula</i> .
Nacellina	Two pairs of salivary glands
Nacelloidea (= Nacellidae)	Lacking crossed-lamellar structures above the myostracum.
Cellana	Inner lateral teeth elongate and beak-like.
Nacella	Epipodial fringe around the periphery of the foot; pallial gill interrupted in front of head; interior shell layer foliated.
Acmaeidea	Wart organs lost; left ctenidium present; licker with smooth medial ridge; two pairs of functional uncini; chromosomes 2n = 10.
Lepetopsina	Osphradium single; eyes lost; three pairs of radular cartilages; ferrous oxides in radular lost; inverted-V radular configuration.
Unnamed Group	Subpallial sensory streaks lost; posterior salivary glands with single pair of ducts; single pair of inner lateral teeth; oral lappets uncini bases vertically aligned; ventral plates combined for inner and outer laterals.
Lepetidae	Loss of eye pigments; outer lateral radular teeth absent; mantle sensory streak present; ctenidium lost; osphradia lost; two pairs of radular cartilages; marginal radular teeth frilled.
Lepetinae	Oesophageal rotation 90°.
Propiliidiinae	Apex directed posteriorly; shell septum internal.
Unnamed Group	Shell microstructure fibrillar; single left ctenidium present; oesophageal rotation 230°.
Acmaeidae	Uncini lost; ventral plates rectangular; anterior shell muscle bundles bulbous.
Acmaeinae	All lateral radular teeth approximately equal in size and shape.
Pectinodontinae	Apex 'dimpled'; outer lateral radular teeth multicuspidate.
Lottiidae	Foliated shell microstructure lost; oral lappets lost.
Patelloidinae	Outer homogenous layer typically absent.
Lottiinae	One pair of uncini lost.

15. PROSOBRANCHS

Taxon	Shell Microstructure				
	Shell exterior			Shell interior	
Patellidae	CFol		ACL	ACL	CFol
Scutellastra	CFol	ACL		ACL	
Nacella	CHom	CFol		CFol	
Cellana	CHom	CFol		ACL	
Acmaea	CHom	CFol	CFib	ACL	ACL
Pectinodonta	CHom	CFol	ACL		ACL
Lepeta	CHom	CFol	ACL		ACL
Propilidium	CHom	CCF		ACL	ACL
Lottiidae	CHom	CFib	ACL		ACL

Figure 15.32 Generalised shell microstructure arrangements of the Patellogastropoda. Taxa are representative members of groups discussed herein and their hypothesised relationships are shown in Figure 15.31. The double line indicates the position of the myostracum. ACL, aragonitic crossed-lamellar; CCF, calcitic coiled fibrillar CFib, calcitic fibrillar; CHom, calcitic homogeneous. (Based on data from MacClintock 1967; Lindberg 1988a; Hedegaard 1990; Lindberg & Hedegaard 1996; Lindberg & Hedegaard unpublished data)

where the lateral teeth attach to the radular membrane). The reduction in the number of teeth does not have any ecological correlatives at higher taxonomic levels. Within some subclades of Acmaeidae and Lottiidae, ecological correlatives of tooth number with diet are apparent, but only after a substantial phyletic reduction in tooth number has already occurred.

Among patellogastropods there is a trend to reduction in the number of gut loops. This same trend is seen in the ontogeny of members of different clades, such that at metamorphosis the gut morphology of apomorphic taxa often resembles that of plesiomorphic groups at adulthood (Lindberg 1988a). Other differences (Patelloidea vs Lottiidae) in hindgut looping patterns were first noted by Dall (1871b), and Fleure (1904) used the diversity of hindgut looping to delineate relationships amongst the Docoglossa (= Patellogastropoda). Walker (1968) examined the ontogeny of gut looping in members of the Lottiidae, the value of gut looping characters in specific determinations, as well as jaw morphology and the looping of the radular sac. More recently, Sasaki (1992) and Sasaki & Okutani (1993a, 1994) have included gut looping characters, jaw morphology and radular sac looping patterns in their studies of Japanese Lottiidae. Lindberg (1986a, 1988b) proposed that the apparent relationships between gut looping complexity and radular morphology result from the developmental linkage of these two structures (Smith 1935; Raven 1966; Lindberg 1983; Verdonk & Cather 1983).

The nervous system of the Patellogastropoda is streptoneurous and consists of four pairs of large ganglia: the cerebral, labial, pleural and pedal. The ganglia are connected by commissures, and from each ganglion nerves radiate to specific regions of the body. The cerebral ganglia innervate the cephalic tentacles, eyes, and statocysts; the labial ganglia are associated with the mouth; nerves from the pleural ganglia branch to the mantle, viscera, osphradia, and nuchal cavity in the Acmaeidae; and the pedal ganglia innervate the foot. In patellogastropods, there is often a second commissure, the 'labral' commissure, connecting the cerebral ganglia in front of the mouth. Angerer & Haszprunar (1996) have suggested that this structure may be diagnostic for patellogastropods.

The sensory structures found in patellogastropods consists of the following: the osphradia, statocysts, eyes, and mantle and cephalic tentacles. The osphradia are located on the ventral floor of the nuchal cavity behind the head and are thought to be important sites of chemoreception (Haszprunar 1985a). In the Patelloidea and Nacelloidea, the osphradia are situated immediately adjacent to the so-called 'Spengel's' or 'wart' organs which structures have been argued to be either apomorphic sense organs (Haszprunar 1988a) or the vestigial rudiments of paired ctenidia (Spengel 1881; Lankester 1883; Stützel 1984). The statocysts, located internally near the pleural ganglia, are orientation structures.

The heart is situated in the pericardial sac, which is located on the left side of the visceral mass directly adjacent to the nuchal cavity. It consists of a single auricle and single ventricle with an aortic bulb; the ventricle is attached to the dorsal surface of the pericardium by a mesocardium. The aorta is divided into a posterior aorta that supplies haemolymph to the viscera, and an anterior aorta that supplies the buccal region, the head, and lastly, the foot. The relative positions of the auricle, ventricle and aorta within the pericardial sac suggest that the patellogastropod heart has been rotated relative to the visceral mass (see Fleure 1904; Lindberg & Ponder 1996 for discussions). The circulatory system lacks capillaries and the venous haemolymph collects in large sinuses before being returned to the auricle via the right kidney.

The excretory system consists of left and right excretory organs (or kidneys). The left excretory organ is next to the nuchal cavity at the centre of the body, and the right excretory organ encircles the visceral mass. The left excretory organ opens directly into the nuchal cavity through a small slit on the left side of the anus, and the right excretory organ connects to the nuchal cavity through a short canal. This canal also functions as a gonoduct. Both excretory organs are connected to the pericardial sac through renopericardial canals.

Most patellogastropods are dioecious although both simultaneous and protandric hermaphroditism does occur in the taxon. Protandry is often correlated with territoriality and it is likely that the Australian species, *Scutellastra chapmani* and *Scutellastra laticostata*, will be found to be protandric hermaphrodites (D.R. Lindberg personal observation). A single gonad (the pretorsional left) is situated under the digestive system. When gravid, the gonad enlarges and forces the visceral mass forward. An anterior gonoduct leads from the gonad into the right excretory organ.

All members of the Patellina broadcast their gametes into the sea, where fertilisation and development take place. Parental brood protection has evolved independently in the Nacellina (Golikov & Kussakin 1972; Lindberg 1981b, 1983). The eggs are retained in the nuchal cavity or in a brood chamber where they are fertilised and develop into crawl-away young; the most highly derived taxa have copulatory structures (Golikov & Kussakin 1972). Stacking, which may increase fertilisation probability, has been reported in several species including *Nacella polaris* from the Subantarctic islands (Picken & Allen 1983).

There have been few studies of patellogastropod development (Smith 1935; Crofts 1955; Dodd 1957; Kay, Corpus & Magruder 1982). The only published study of the development of Australian species is that by Anderson (1966). Larval development passes rapidly through the trochophore stage, and the veliger spends only about seven days in the plankton. However, metamorphosis does not occur immediately when the veliger settles to the bottom, and the veliger may swim periodically for up to 10 days. Metamorphosis occurs during the 10th to the 15th day. Time from fertilisation to a completely developed juvenile limpet averages about 40 days. Lottiid species become sexually mature at much smaller relative shell sizes than patelloidean species: whereas patelloidean species become sexually mature at about 45% of their average adult shell length, lottiid species attain sexual maturity at about 24% of their average adult shell length (data analysed from Powell 1973; Branch 1974a, 1974b; Nicotri 1974).

In determining phylogenies, patellogastropod systematists have used karyotypic data (Nishikawa 1962; Chapin & Roberts 1980; Nakamura 1986); electrophoretic data – for populations of some species (Gresham & Tracey 1975; Murphy 1975; Sly 1984); data from detailed studies of specific organ systems and structures (Haszprunar 1985a; Hodgson & Bernard 1988; Marshall & Hodgson 1990; Jamieson, Hodgson & Bernard 1991); body pigmentation patterns (Dall 1871b; McLean 1966; Lindberg 1981c); ecological characters (Golikov & Kussakin 1972; Branch 1976); and behavioural characters (Branch 1975a).

Patellogastropod limpets are the ‘guinea pigs’ of rocky shore ecologists. They are primary consumers in the food chain, easily manipulated and marked, and predominantly sessile; they are also characteristic of specific tidal zones and habitats over extensive regional areas. Well documented and detailed ecological studies using patellogastropods as the study organism have been conducted throughout the world including England, southern Africa, North America, New Zealand and Australia. In Australia, it was problematic identifications of limpets in the early ecological studies of the late 1940s and early 1950s that persuaded Macpherson (1955) to undertake her systematic revision of the Australian patellogastropod fauna, and 25 years later a similar impetus brought Ponder & Creese (1980) together for the most recent revision.

Many of the ecological studies of Australian patellogastropods have been conducted during the last 20 years by A.J. Underwood of the University of Sydney and his students. These studies have focused on reproductive biology and life history (Underwood 1974; Black 1977; Creese 1980b, 1981; Parry 1982a, 1982b; Fletcher 1984a, 1984b, 1987; 1988a), dispersion and behaviour (Underwood 1975b, 1976a, 1976b, 1977; Mackay & Underwood 1977; Creese 1980a, 1982; Mapstone, Underwood & Creese 1984), limpet/algal interactions (Underwood 1976a, 1984; Jernakoff 1985a, 1985b; Arrontes & Underwood 1991), competition (Underwood 1978; Black 1979; Creese & Underwood 1982; Fletcher & Creese 1985; Fletcher & Underwood 1987) and physiology (Parry 1978). It is interesting to note that most of these studies have examined either nacelloidean or lottiid species. Patelloideans, which have been the subject of extensive studies in both England and southern Africa have been virtually ignored in Australia until recently (Scheibling & Black 1993). Seagrass associates (*Asteracmea* species) have also gone unreported despite considerable work in Australian seagrass communities (Walker & Prince 1987; Walker, Kendrick & McComb 1988).

Ecologically, the Australian limpets represent one of the best studied patellogastropod faunas in the world, although as noted above, several notable exceptions remain. *Asteracmea crebristriata* has been reported to be a seagrass-associated limpet (Cotton 1959a), but habitats for other *Asteracmea* species are not known, although the minute shells are relatively common in beach drift. Similarly, despite the fact that literally thousands of shells of *Propilidium tasmanicum* have been collected from Sydney Harbour, only a single live specimen has ever been found and its microhabitat remains a mystery.

The Australian patellogastropod fauna undoubtedly represents an aggregation of lineages accumulated through geological time and subjected to the vagaries of colonisation, origination, radiation, and extinction. Like the fauna of southern Africa, the Australian fauna, is diverse and includes representatives of patelloidean, nacelloidean and acmaeoidean lineages. In Chile, only nacelloidean and acmaeoidean lineages are present, and in Europe only acmaeoidean and patelloidean taxa, and only acmaeoidean species are found along the coast of western North America. Although it is tempting to compare and contrast data for ‘limpets’ co-occurring in the same intertidal habitat (as well as between continents), it is important to remember that the different patellogastropod clades have unique histories. Moreover, current taxonomic allocations often do not reflect the evolutionary relationships between species. Biological studies and experimental designs that consider the phylogenetic history of the group will undoubtedly provide greater resolution for biologists studying the habits of these and other molluscs.

Most patellogastropods occur on rock (Pl. 22.2); their form is relatively conservative. Aperture shapes range from elongate-oval to circular; apex position varies from central to strongly anterior; and shell length:shell height ratios provide no distinctive ranges of variation. Exterior shell sculpture ranges from fine riblets to large coarse radial ribs and/or concentric sculpture.

Patellogastropods associated with calcareous substrata are often distinguished by medium to high, conic, unicoloured (white-pink) shells with circular apices; sculpture is often subdued with concentric growth lines predominant. However, there are enough exceptions to this general pattern to make the identification of carbonate-associated limpets in the fossil record dubious. Extant carbonate-associated species are quite common. In Australia, *Patelloida nigrosulcata* is such a species occurring on abalones and limpets. Often when living on other invertebrates distinctive aperture shapes are produced and the limpet’s growth rate appears to be correlated with the growth rate of the host (Lindberg & Pearse 1990; Scheibling, Evans, Mulvey, Lebel, Williams & Holland 1990).

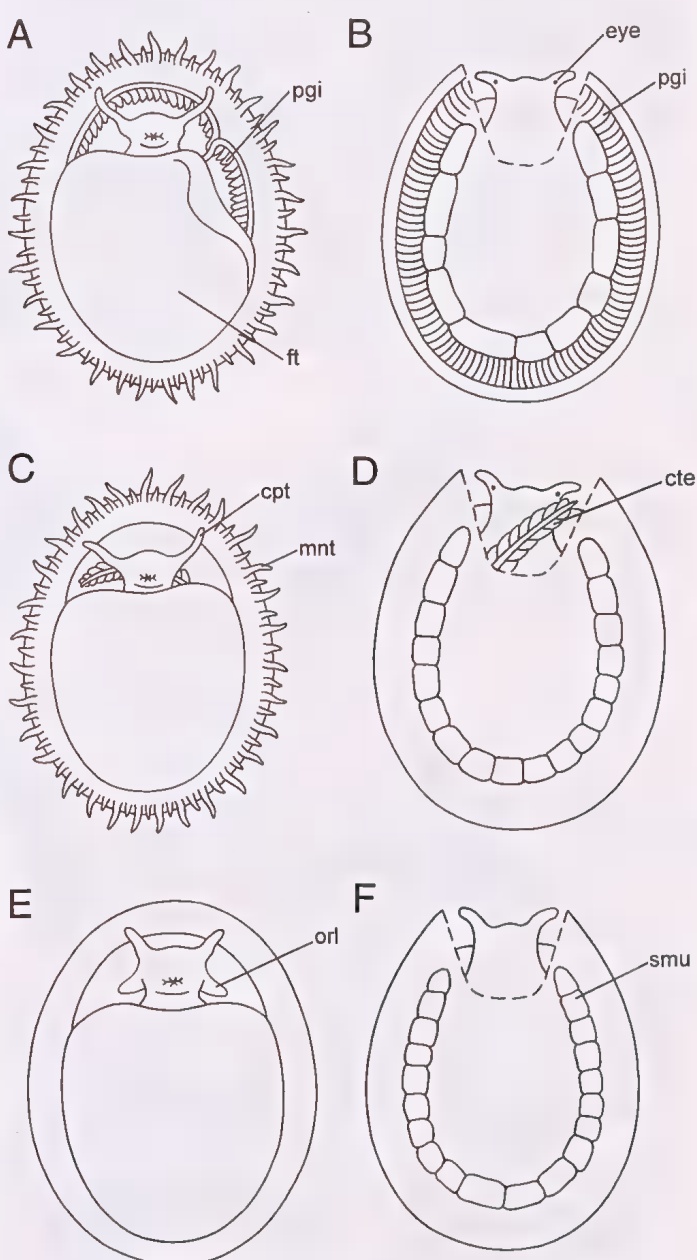


Figure 15.33 Order Patellogastropoda. External anatomy of representative patellogastropod taxa. A, B, Patelloidea and Nacelloidea; C, D, Lottiidae; E, F, Lepetidae. A, C, E, ventral views; B, D, F, dorsal views with shell removed and mantle removed over nuchal cavity. cpt, cephalic tentacle; cte, ctenidium; eye, eye; ft, foot; mnt, mantle tentacle; orl, oral lappet; pgi, pallial gill; smu, shell muscle. (After Lindberg 1988b) [R. Plant]

15. PROSOBRANCHS

Worldwide, numerous extant patellogastropod species utilise specific types of plants as substrata. No limpet is known to live on any species of Chlorophyta (green algae). The Laminariales and Fucales of the Phaeophyta (brown algae), and only the Cryptonemiales (corallines) among the Rhodophyta (red algae), as well as many species of seagrasses (Zosteraceae, Angiospermae) serve as substrata for stenotopic limpets. The geographic distribution of extant marine plant limpets is cosmopolitan; they occur in all major oceans except the Arctic. In Australia, the best known seagrass limpet is *Naccula punctata* although *Asteracmea* species have been reported to be associated with seagrasses as well (Cotton 1959a). Marine plant limpets are readily identifiable by their distinctive shell morphology which typically features parallel lateral shell margins and elevated anterior and posterior portions of the aperture (Fig. 15.36A, B). Often the range of morphological variation present in these stenotopic species is correlated with the range of variation present in the host plant (Lindberg 1982, 1990b), and because of their distinctive and conservative morphology, marine plant limpets are easily recognised in the fossil record. In contrast to marine plant limpets that occur on angiosperms and branching corallines, those that occur on laminarians and fucoids appear to have evolved relatively recently. All patellogastropods that use these latter taxa as host substrata are extant, and when present in the fossil record they date only from the late Pliocene and Pleistocene. Generally, no Australian species are found on algae.

There appears to be little to no economic interest in Australian patellogastropods, although *Cellana* species are a significant fishery in other regions (for example, Hawaii, Kay *et al.* 1982). Aboriginal usage of nearshore molluscs have been documented (for example, Henderson 1986), and the larger intertidal patellogastropod species were commonly procured food items. D.R. Lindberg (personal

observation) has noted *Cellana solida* and other *Cellana* species in midden deposits from Tasmania and New South Wales. In conservation and bio-monitoring applications, Povey & Keough (1991) have used *Patelloida* species and *Cellana tramoserica* to assess the effects of human trampling on Australian rocky shores.

The biogeography of the Australian patellogastropod fauna is complex. The fauna contains components of relict Tethyan distributions, as well as cosmopolitan taxa, and endemics with short ranges. Species of *Scutellastra* extend eastward from southern Africa to the tropical eastern Pacific and are found on most of the rocky shores of Australia. During the Miocene this genus also occurred in New Zealand (Powell 1973). A similar Tethyan distribution is exhibited by *Cellana*. Although their current distribution excludes the shores of the eastern Pacific, large *Cellana* species were important components in Tertiary communities in both North and South America (Lindberg & Hickman 1986). Tethyan distributions are also apparent for members of the Pectinodonta and the genus *Asteracmea*. Pectinodontina taxa range from the east coast of Australia and the island groups of the western Pacific to the tropical eastern Pacific, the Caribbean and eastern Atlantic. *Asteracmea* species range from the Red Sea throughout Australasia and west to the Caribbean.

The patellogastropod fossil record reveals previously unsuspected patterns of radiations, persistences and extinctions within clades. The fossil record can be used to explain the distributions of present 'outliers', and why such taxa are related to groups no longer in the area despite ecological convergence with the more diverse modern groups currently occupying the region. These data are only possible because diagnostic characters are preserved in the fossils. Without shell structure characters, the fossil record of the Patellogastropoda would be

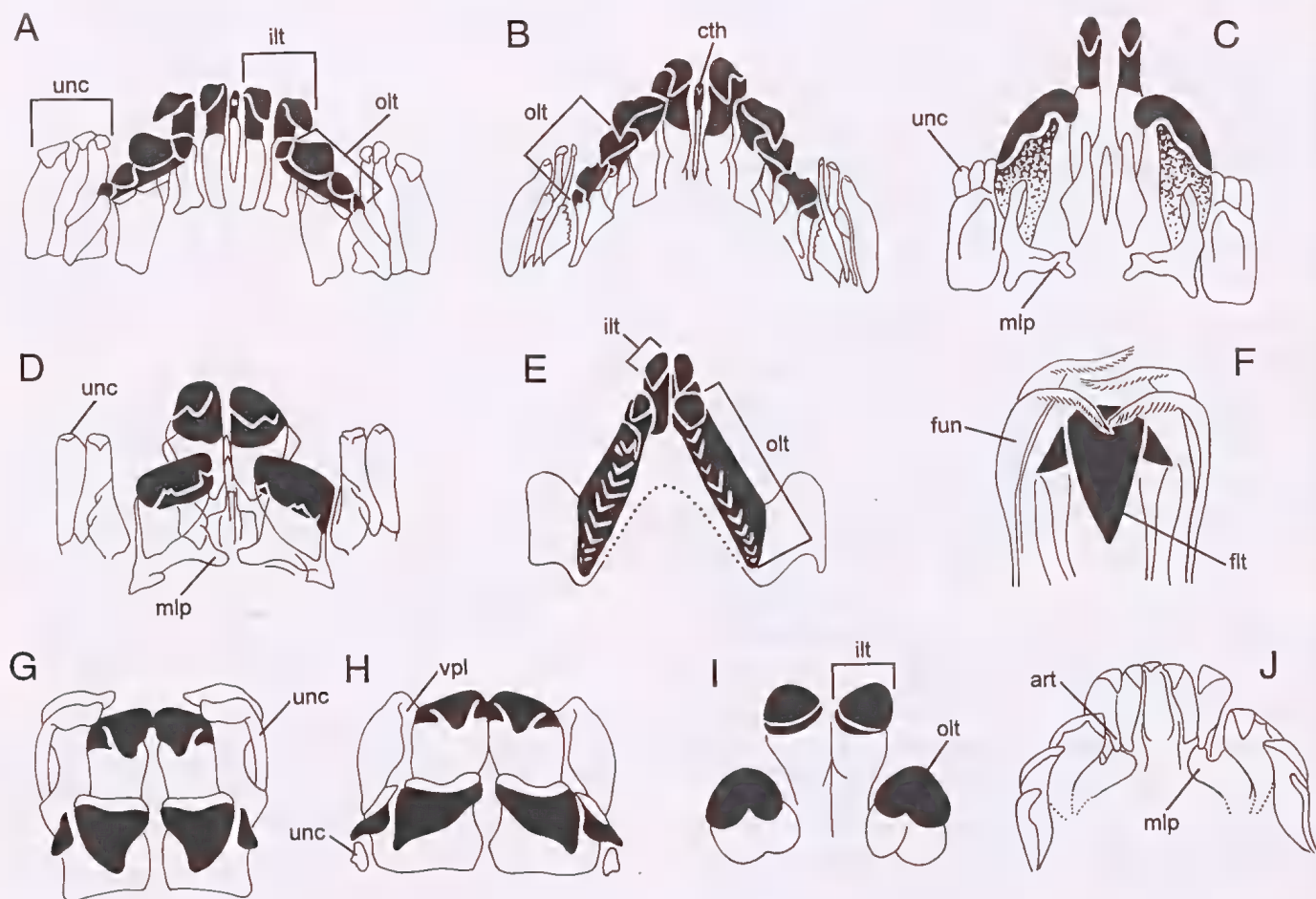


Figure 15.34 Representative radular configurations in the Patellogastropoda. A, *Scutellastra* and Patellidae (in part). B, *Cymbula* (Patellidae). C, *Cellana* (Nacellidae). D, *Nacella* (Nacellidae). E, *Pectinodonta* (Acmaeidae). F, *Propilidium* (Lepetidae). G, *Patelloida* (Lottiidae). H, *Lottia* (Lottiidae). I, *Asteracmea* (Lottiidae). J, *Neoleptopsis* (Neoleptopsidae). Dark shading indicates distribution of ferrous oxides in lateral teeth. art, articulation cusp; cth, central tooth; flt, fused first pair of lateral teeth; fun, functional uncini; ilt, inner lateral tooth/teeth; mlp, medial lateral process; olt, outer lateral tooth/teeth; unc, uncini; vpl, ventral plate. (A–D, after Powell 1973; F, after Pilsbry 1891; G, H, after Golikov & Kussakin 1972; J, after McLean 1990)

[R. Plant]

little more than an amalgamation of conical shells. Numerous nominal patellogastropod taxa are recorded from the Palaeozoic (for example, *Floripatella*, *Palaeoscurria*, *Lepetopsis*) and Mesozoic (for example, *Scurriopsis*, *Conorhytis*, *Hennocquia*) (Knight, Cox, Keen, Batten, Yochelson & Robertson 1960a; Yochelson 1988). The earliest patellogastropod verified from shell structure is *Patella costulata* from the Triassic of Italy (Hedegaard, Bandel & Lindberg in press). However, it is in the late Cretaceous and Tertiary that many of the extant higher taxa have their first appearance in the fossil record (Lindberg 1988a). Recently, Kase (1994) used shell microstructures to recognise patelloidean limpets from the Miocene-Pliocene of Japan; Patelloidea are absent from the Recent north-western Pacific Ocean. In Australia and New Zealand, patellogastropods are known primarily from Tertiary deposits, however Powell (1973) has suggested that *Cellana carpentariana* from the lower Cretaceous of the Northern Territory is the earliest representative of the Nacelloidea. Oliver (1926) described *Actinoleuca multiradialis* from the Oligocene of Victoria, and Chapman & Gabriel (1923) described *Cellana* and *Patelloida* species from the Miocene of Victoria. In addition to these published records, fossil patellogastropods are known to be present in the Pliocene of Western Australia (D.R. Lindberg personal observation).

Suborder PATELLINA

Superfamily PATELLOIDEA

Members of the Patelloidea exhibit some of the most primitive character states of the living Patellogastropoda. These include a patelliform shell with an essentially central apex, nine pairs of chromosomes, calcitic foliate shell microstructures, a branchial cordon (pallial gills), and a radula with three pairs of uncini and a central lateral field with two pairs of inner lateral teeth (Fig. 15.34A, B). Shell sculpture is primarily radial, often forming robust ribs. Concentric shell sculpture is typically limited to rugose growth lines. Patelloideans are the largest of all patellogastropods, reaching shell lengths in excess of 350 mm.

Traditionally, the taxon Patelloidea (or Patellidae) included all patellogastropods with a branchial cordon and three pairs of uncini – the Patellinae and Nacellinae (Thiele 1929–1935; Christiaens 1973; Powell 1973). Phylogenetic analysis of the patellogastropods reveals that these characters are plesiomorphic (*i.e.* primitive characters for the group). Rather than sharing a common ancestor with the Patelloidea, the Nacelloidea share a common ancestor with the Acmaeoidea (Fig. 15.31). Based on this finding, Lindberg (1988a) removed Nacelloidea (Nacellinae) from the Patelloidea, placing it together with the Acmaeoidea in the clade Nacellina (Fig. 15.31; Table 15.2). That action left Patelloidea as a monophyletic group comprising two sub-groups – the Patellidae and an unnamed group typified by species of *Scutellastra* (see below under Patellidae).

The highest diversity of Patelloidea species in the world occurs along the rocky shores of southern Africa where patelloids have been studied extensively by G.M. Branch and his colleagues (see Branch 1981 and references therein). This southern African fauna is composed of members of both the Patellidae and *Scutellastra* subclades. In western Europe, the patelloidean fauna is composed solely of members of the Patellidae, whereas in Australia all four species are members of the *Scutellastra* group. Most Patelloidea species occur in intertidal habitats, although some of the largest species such as *Scutellastra kermadecensis* and *S. tabularis* are found just below the limits of lower low water.

Patelloidean species, because of their large size, have been important components of aboriginal diets for over 150 000 years. Human predation reduces both maximum and mean limpet size at some localities (Speed 1969; Parkington 1977). Patelloidean species are also being used in biological monitoring studies on the health of rocky shore communities because of their ubiquitous presence and ecological role (Hockey & Bosman 1986; Povey & Keough 1991).

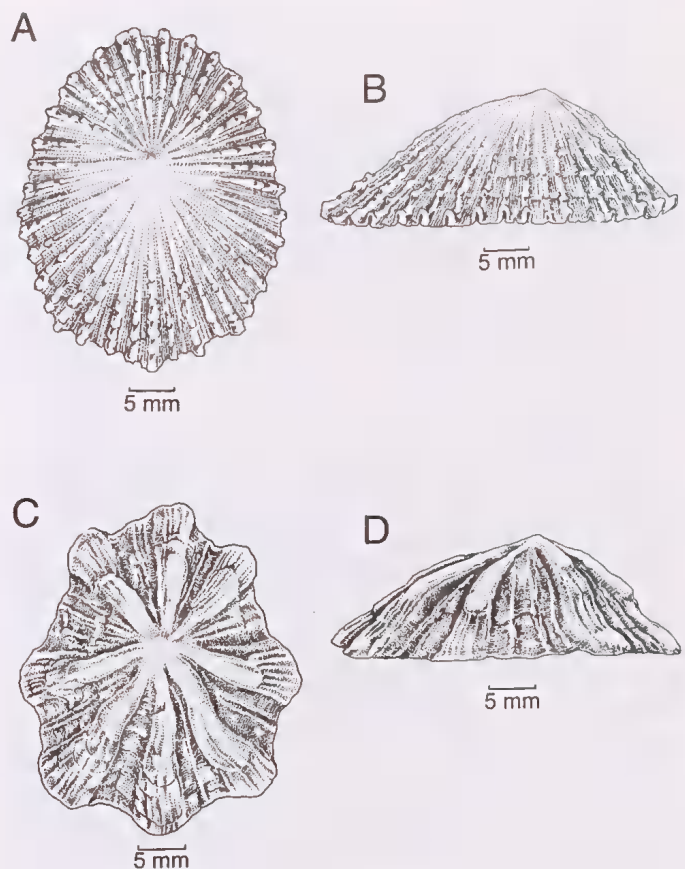


Figure 15.35 Family Patellidae. Shells of Australian species: A, B, *Scutellastra peronii*; C, D, *Scutellastra chapmani*. A, C, dorsal view; B, D, lateral view. [R. Plant]

Lindberg (1988a) restricted the Patelloidea to a monophyletic group, however, groupings within this clade are not yet delimited rigorously and numerous workers, including Thiele (1929–1935), Koch (1949), Christiaens (1973) and Powell (1973), have recognised as many as fourteen taxonomic divisions within the Patellidae alone. Many of the proposed genera are monotypic.

Family Patellidae

As discussed above under Patelloidea, extant members of the Patellidae are restricted to the eastern Atlantic margin and southern Africa. They are diagnosed by features of shell microstructure and include groups with both stepped and diverging radular configurations (Fig. 15.34A, B). Shell microstructures are predominantly foliated (Fig. 15.32). The genera *Patella*, *Cymbula* and *Helcion* are members of this family.

Patellids are found primarily in temperate regions and have been observed and written about since the time of Aristotle. They have been the subject of extensive natural history and ecological studies, especially in the United Kingdom, the long familiarity undoubtedly contributing to an underestimate of their evolutionary diversity. Moreover, because 'patellid' species are ubiquitous throughout the world, it was assumed that their ecological, physiological, and behavioural traits are undistinguished. Traits specific to either Patellidae or *Scutellastra* subgroups often went unrecognised. No members of the Patellidae *sensu stricto* occur in Australia.

Members of the *Scutellastra* group are diagnosed by lateral teeth arranged in a stepped configuration (Fig. 15.34A), and a shell structure that is dominated by crossed-lamellar shell microstructures. All of these characters are thought to represent plesiomorphic (or ancestral states) for the Patellogastropoda and the possibility that this group is paraphyletic cannot be ruled out at this time.

15. PROSOBRANCHS

All four Australian 'patellid' species belong to this taxon – *Scutellastra flexuosa*, *S. peronii* (Fig. 15.35A, B), *S. chapmani* (Fig. 15.35C, D) and *S. laticostata*; the last three are Australian endemics. The Australian taxa, *Patellanax* and *Penepatella*, established by Iredale (1924, 1929a), are synonyms of *Scutellastra*; both Macpherson (1955) and Cotton (1959a) assigned all the Australian patelloideans to the genus *Patellanax*. Members of the *Scutellastra* group are found throughout the Indo-West Pacific, southern Africa, and even in the tropical eastern Pacific. The endemic Australian species are the most temperate members of the group. In contrast, *S. flexuosa* is found in the tropical regions of northern Australia and as far north as Okinawa; this tropical/warm temperate habitat is more typical of the group.

The members of the *Scutellastra* group have been studied extensively by G.M. Branch in southern Africa (see Branch 1981 and references therein). Ecologically the clade is characterised by combinations of traits, including being restricted to specific intertidal zones, exhibiting aggressive behaviour towards conspecifics, having low gonad output, territorial defence, sharp adult/juvenile differentiation and being protandrous (see also Creese, Schiel & Kingsford 1990). Although the Australian species have not been studied as comprehensively as the southern African species, there are noticeable similarities in the habits of members of the two faunas. For example, *S. laticostata* is restricted to low zone, wave exposed benches where it maintains distinct home sites. *Scutellastra chapmani* is also restricted to low intertidal habitats and appears to feed exclusively on coralline algae; it also appears to be a protandric hermaphrodite (Lindberg unpublished data). From impressions of its irregular shell margins on the substratum, *S. flexuosa*, which is another carbonate-associated species, appears to form a specific home site.

Suborder NACELLINA

Members of the Nacellina are diagnosed by a reduced terminal chromosome, increased length of the radula, reduced length of the hindgut, the presence of an outer calcitic homogeneous shell layer (Fig. 15.32), the reduction of the inner radular tooth field from two pairs of teeth to one pair of teeth (Fig. 15.34C, D), and reduction and increased fusion in the outer lateral teeth. This group is also diagnosed by the formation of distinct segments for each tooth row (Macpherson 1955) and increasing development of supporting plate structures for the individual teeth.

As discussed above, Lindberg (1988a) first proposed this taxon to accommodate the Nacellinae (*sensu* Powell 1973) which he removed from the Patellidae, thereby rendering the Patelloidea monophyletic. Previous classifications that united patelloideans and nacelloideans were based on shared primitive characters such as the number of uncini (three pairs) and the presence of a branchial cordon in the mantle groove. Because of the spurious grouping of nacelloideans with patelloideans (rather than with acmaeideans), most publications treating Australian patellogastropods (Oliver 1926; Powell 1973; Christiaens 1975a, 1975b; Ponder & Creese 1980) have not discussed this taxon. Only Macpherson (1955) treated both the Australian 'Patellidae' (*Patella* + *Cellana*) and 'Acmaeidae' in the same publication.

Like the Patelloidea, most Nacellina species occur in rocky, marine intertidal habitats. Unlike the Patelloidea, Nacellina species have invaded offshore habitats and others have successfully invaded brackish water habitats (Ponder & Creese 1980; Marshall 1985; Lindberg 1988a, 1990a). Members of the Nacellina are the only living patellogastropods that have invaded polar regions and the deep sea, including hydrothermal vents (Lindberg 1988c; McLean 1990). With the exception of northern Europe and southern Africa, most of the patellogastropod faunas of the world are dominated by members of the Nacellina, and over 85% of Australian patellogastropods are members of this clade. It is therefore not surprising that Nacellina species have figured predominantly in rocky shore ecological studies.

Here the Nacellina are divided into two groups – the Nacelloidea with *Nacella* and *Cellana*, and the Acmaeidea which includes the Lottiidae, Acmaeidae, Lepetidae, and Lepetopsina.

Superfamily NACELLOIDEA

Family Nacellidae

In the Nacellidae, the percentage of crossed-lamellar shell material is reduced and calcitic foliated structures have increased (Fig. 15.32). It is the predominance of these foliated structures that gives this group the nacreous-like interior shell surface. There is also an increase in the degree of fusion of the outer lateral teeth, and the development of tooth plate structures (Fig. 15.34C, D); median fusion of the inner lateral teeth is vestigial. Although fusions in the outer lateral tooth field are sometimes difficult to demarcate within the cusps, the vestiges of these former distinct teeth are visible in the basal tooth plate structures. The radula also obtains its maximum length relative to shell length in members of this group.

Workers in Australia and elsewhere have traditionally included these taxa within the Patelloidea (Macpherson 1955; Cotton 1959a; Powell 1973) as some sort of modified 'patellid'. This was done because of the over emphasis on the characters of the branchial cordon and radula – all of which are plesiomorphic or ancestral character states. However, other characters suggested relationships with the Acmaeidea, and were obvious enough to prompt Macpherson (1955) to state that '*Cellana* is obviously intermediate in radular characters and suggests that further study including anatomical dissection might prove it to be the stock of Patellidae from which Acmaeidae sprang'.

Nacellid species are exclusively marine and occur predominantly in the intertidal and nearshore habitats. This group is also represented in the deep sea by species of *Bathycyma* (Okutani, Tsuchida & Fujikura 1992; Lindberg unpublished data). There is a strong biogeographical distinction between the two groups that make up this family. Typically, *Nacella* is widely distributed throughout the Subantarctic and extends out of this region only along the west coast of South America to central Chile; the highest diversity of *Nacella* species is found at the tip of South America. In contrast, the group including *Cellana* is almost exclusively tropical to warm temperate in distribution, and overlaps with the *Nacella* group only in the southernmost islands of New Zealand.

In Australia, the genus *Cellana* is represented by both cosmopolitan tropical species and temperate endemic species. The two Australian *Nacella* species are on islands in the Subantarctic region. Unpublished shell structure studies by Lindberg & Hedegaard on the Australian seagrass limpet *Naccula punctata* (Fig. 15.36A, B) suggest that this species may be a representative of a highly derived nacelloidean taxon, not an acmaeidean as generally thought.

The genus *Cellana* is diagnosed by elongation of both the inner and outer lateral teeth of the radula (Fig. 15.34C). Elongation in the outer lateral field masks the involvement of other distal outer lateral teeth in the formation of this complex although they are represented by small cusps along the outer surface of the teeth. In *Cellana turbator* from tropical north-eastern Australia, there is a small cusp on the outer edge of the inner lateral teeth as well (Macpherson 1955). Whether this is a true bifid cusp or the remains of a fusion with a more distal inner lateral tooth is not known. Uncini vary between three and two although in this latter situation cusplless plates are present; the median fusion of the inner lateral teeth is vestigial. *Cellana* has crossed-lamellar shell structures inside the myostracum, but most of the shell is composed of foliated shell structures (Fig. 15.32). The radula also obtains its maximum length relative to shell length, and the branchial cordon is complete over the head region.

Cellana is represented in Australia possibly by as many as eight species, distributed from tropical north-eastern Queensland to temperate South Australia and Tasmania. It is absent from south-western and western Australia. In northern Australia it is represented by widely distributed tropical taxa such as *Cellana radiata* and *C. testudinaria*. The remaining Australian *Cellana* species – *C. conciliata*, *C. turbator*, *C. tramoserica* (Pls 22.1, 22.2), *C. solida* – are endemic and two species – *C. analogia* and *C. howensis* – occur only at Lord Howe Island.

Cellana tramoserica (Fig. 15.36C, D) has figured predominantly in intertidal research in Australia. Studies include those of Underwood (1975b), MacKay & Underwood (1977), Parry (1978), Branch & Branch (1980a), Creese & Underwood (1982), Fletcher (1984a, 1984b), Underwood & Verstegen (1988), Petraitis (1992),

Beovich & Quinn (1992), and Marshall & Keough (1994). This species has been used to assess ecological damage to Australian rocky shores (Povey & Keough 1991; Keough, Quinn & King 1993). With the exception of a few small studies in New Zealand (see Creese 1988), Japan (Iwasaki 1992), Hong Kong (Liu 1994a, 1994b) and southern Africa (Branch 1975b; Lasiak 1990, 1993; Lasiak & White 1993), most of our knowledge of ecology, behaviour and reproduction *Cellana* species comes from the Australian fauna. However, no modern systematic treatment of the group is available and the only monographic works are taxonomic treatments by Pilsbry (1891) and Powell (1973). Kay (1979) found that *Cellana* in the tropical Pacific is present primarily on high islands and is absent from coral atolls. A similar association also seems to be likely for the fossil taxa from the New World (see below). However, both the Australian and New Zealand species are associated with a wide variety of habitats including both sedimentary and carbonate substrata. Although there is no commercial harvest of *Cellana* species in Australia, members of the taxon are the basis of a US\$1 500 000 per annum commercial fishery in Hawaii (unpublished data, Hawaii Aquaculture Development Program).

Cellana species reached their greatest diversity in the Holocene in the Australasian region. No Holocene species occur in the New World; the closest is a single species on the oceanic Juan Fernandez Island, 650 km off the coast of Chile (Powell 1973). However, during the Tertiary the subfamily was present along the coast of North America and also along the coast of South America. Lindberg & Hickman (1986) described the large (150+ mm) *Cellana ampla* from the Eocene of Oregon, United States of America (38 mya), and re-assigned another large (200+ mm) species, *Patella fuezalidai* from the Pliocene of Chile, to this taxon on the basis on shell structure. Chapman & Gabriel (1923) described two fossil species from the Late Tertiary of Victoria as *Cellana* species and Skwarko (1966) tentatively placed a Cretaceous species from the Northern Territory in this taxon. However, in the absence of information on shell structure, assignment of these species to a specific clade within the Patellogastropoda is problematic.

The genus *Nacella* is diagnosed by shells composed almost entirely of foliated shell structures (Fig. 15.32), an epipodial fringe around the periphery of the foot, and branchial cordon interrupted over the head region. Crossed-lamellar structures, if present at all, are restricted to thin layers just below the myostracum. The lateral teeth are elongate as in species of *Cellana*, but less so (Fig. 15.34D). Both inner and out lateral tooth fields exhibit more distinct fusion of teeth than is seen in species of *Cellana*, and the basal plate structures are more complex. A vestigial medial fusion of the innermost inner lateral teeth is present as in *Cellana* and the uncini vary from three pairs to two pairs and a plate. Implicit in many taxonomic treatments is the placement of the *Nacella* species after *Cellana* species because of the former's 'specialised' habitat (the cold southern polar region) and the presence of the unique epipodial fringe. However, the radular and gill characters of both groups are plesiomorphic and shared with the Patelloidea. The remaining specialised *Nacella* characters (epipodial fringe, shell structure, habitat) are unique (autapomorphies) and therefore tell us little about relationships although they are useful for distinguishing members of the Nacellidae.

Nacella is not represented on continental Australia, but *Nacella macquariensis* (Fig. 15.36E, F) occurs at Heard and Macquarie Islands. Except for some limited work on *Nacella concinna* (Shabica 1971; Picken & Allen 1983), and examination by Simpson of aspects of the ecology of *N. macquariensis* at Macquarie Island (Simpson 1976) and the relationship between allometric growth and habitat (Simpson 1985), little is known of *Nacella* species. They occur exclusively in intertidal and nearshore habitats; many species are associated with large brown algae (Powell 1973).

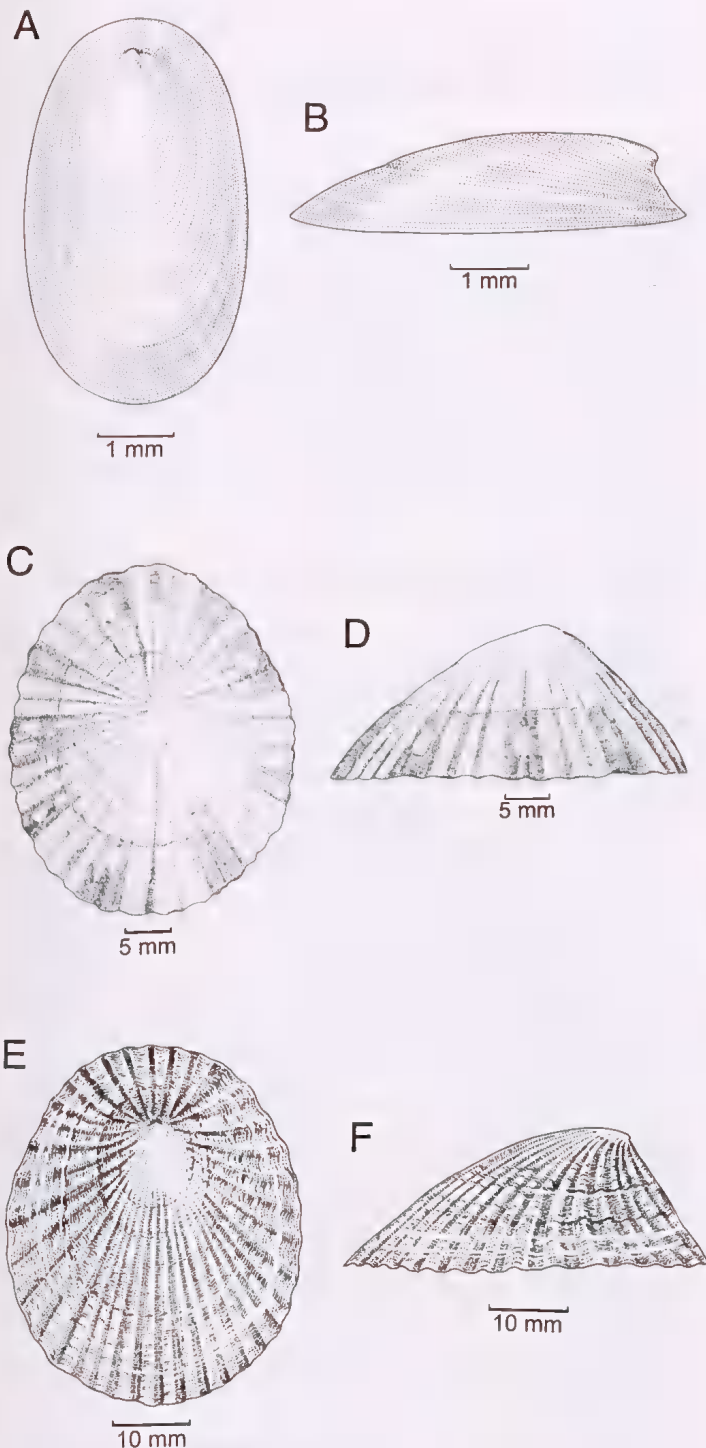


Figure 15.36 Family Nacellidae. Shells of Australian species: A, B, *Nacella punctata*; C, D, *Cellana tramoserica*; E, F, *Nacella macquariensis*. A, C, E, dorsal view; B, D, F, lateral view.

[A, B, E, F, R. Plant; C, D, S. Weidland]

Superfamily ACMAEOIDEA

Members of the Acmaeoidea are diagnosed by ten pairs of chromosomes, the presence of a single gill in the nuchal cavity (Fig. 15.33C, D) and two pairs of uncini. As in the sister taxon Nacelloidea, there is only a single pair of inner lateral teeth, typically unfused. Each outer lateral tooth field comprises a close juxtaposition of two teeth although this combination is often referred to as a single bicuspidate tooth (for example, Ponder & Creese 1980). However, as demonstrated by Lindberg & McLean (1981) each of these supposed 'cusps' resides on its own distinct basal plate, and although closely aligned, their bases remain distinct and reveal the presence of two teeth. There is a maximum of two pairs of uncini, but they have been lost independently in many groups (Fig. 15.34E–J).

Australian workers were among the first to notice substantial differences between taxa allocated to the 'universal genus' *Acmaea* to which all Acmaeoidea were assigned. Both Iredale (1915) and Oliver (1926) proposed generic rank taxa. Iredale's were based on shell morphology, but Oliver incorporated shell, radula, and gill characters in his classification. Other workers around the world have followed with anatomical and shell morphology studies on their own fauna, and this once homogeneous group is now interpreted as a diverse complex of lineages. It is not unusual to find representatives of three to six distinct lineages of Acmaeoidea co-occurring in any given region (Lindberg 1988a). Australia is no exception with at least four subclades of Acmaeoidea represented here.

Acmaeoidea species are primarily marine and occur predominantly in the intertidal and nearshore habitats (Lindberg 1988a). The group is represented in the deep sea by members of the Lepetopsina, Pectinodontinae and Lepetidae. Species diversity in these deep-sea clades is extremely low in the Australian region, there being typically only one or two representatives of each clade (the Lepetopsina are not known from Australia). Intertidal genera are often speciose. There are no strong biogeographical trends within Acmaeoidea. Congeners may range from cool temperate to tropical habitats.

The Lepetopsina was described by McLean (1990) as the sister taxon of all other patellogastropods. This placement was based on a small number of radular characters (see Fig. 15.34J, *Neoleptopsis*), and he assumed that the contradictory evidence from anatomical and shell microstructure characters resulted from convergence. The primary radular character was tooth articulation – a supposed plesiomorphic character found in Polyplacophora (chitons) and monoplacophoran outgroups. However, the structures producing the articulation in the Lepetopsina are not known in either the Polyplacophora, monoplacophorans or even in other gastropod taxa (Hickman 1983; McLean 1990). Moreover, the medial lateral projections that articulate with the second lateral teeth in some Lepetopsina taxa are also found in the Nacelloidea (Fig. 15.34C, D) suggesting that this form of articulation is apomorphic in the Patellogastropoda. In contrast to McLean's placement, Fretter (1990) studying the anatomy of five species of Lepetopsina emphasised characters shared with other acmaeoidean taxa and concluded that they are closer to the 'Acmaeacea' than the 'Patellacea' (V. Fretter personal communication; McLean 1990). Phylogenetic analysis supports Fretter's conclusion (Fig. 15.31) and thus, Lepetopsina is considered here under superfamily Acmaeoidea. Lepetopsina species are known from hydrothermal vent and seep communities in the North Pacific and off of the west coast of Florida (McLean 1990). None is known to occur in the Australasian region.

Family Acmaeidae

Members of the Acmaeidae are diagnosed by the co-occurrence of foliated and fibrillar prismatic shell microstructures, robust and simple radular segments with associated basal tooth plates arranged in chevrons and lack of uncini. All living members of this group have white shells that are devoid of markings.

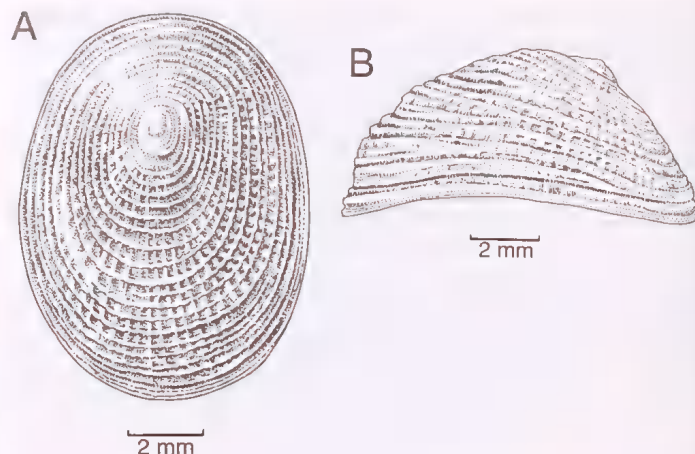


Figure 15.37 Family Acmaeidae, subfamily Pectinodontinae. *Pectinodonta kapalae*, shell: A, dorsal view; B, lateral view. [R. Plant]

For more than 100 years this taxon included all patellogastropods with a ctenidium, and most Australian workers followed this usage (Macpherson 1955; Cotton 1959a, Ponder & Creese 1980; but see Oliver 1926). Lindberg (1986b) reinstated the senior synonym Lottiidae for almost all taxa assigned to the Acmaeidae, and restricted the usage of Acmaeidae to a small monophyletic group of limpets that share their most recent common ancestor with the north-eastern Pacific species *Acmaea mitra*.

Acmaeidae are distributed throughout the world's oceans, but are not known from Antarctica. Two subfamilies are recognised – the Acmaeinae and Pectinodontinae; the latter occurs in Australian waters.

Subfamily Pectinodontinae

The shell of pectinodontines typically has prominent radial and concentric sculpture which gives it a cancellate appearance (Fig. 15.37A, B). This form of sculpturing is uncommon in other nearshore patellogastropod taxa. Shells with only concentric growth lines do occur; known fossil species are also much less cancellate than living taxa (Marshall 1985; Lindberg & Hedegaard 1996). Apex position varies from just slightly anterior of centre to the anterior quarter of the shell. Most specimens also show a characteristic early growth phase in which apertural surface area expands rapidly with little increase in shell height. After this initial phase of rapid dilation subsequent shell growth is more equally divided between apertural increase and increase in shell height. It is this ontogenetic change that produces the dimpled apex characteristic of pectinodontine species (Fig. 15.37A, B). The pectinodontine shell is composed of four shell microstructure units – the exterior layer is homogeneous and followed by a narrow foliated layer, a commarginal crossed-lamellar layer, the myostracum, and a complex crossed-lamellar layer (Fig. 15.32). The radular tooth morphology is unique among patellogastropods (Fig. 15.34E). The inner lateral tooth is unicuspidate, the second lateral is uni- or bicuspidate, and the exterior outer lateral tooth is multicuspidate with between seven and twelve cusps per tooth. All three teeth are in close juxtaposition forming a narrow, inverted V-shaped, row alignment.

Pectinodontine species are found on wood and vestimentiferan tubes. Olsson (1971) first reported the association of pectinodontine species with wood. Christiaens' (1979) is the only comprehensive review of the group and Marshall (1985) reviewed the fossil and living taxa of New Zealand and New South Wales. Recently, Okutani *et al.* (1992) proposed the genus *Serradonta* for a pectinodontine from the tube of a vestimentiferan. *Serradonta* is distinguished from *Pectinodonta* by the presence of a

multicuspidate median lateral tooth. Lindberg & Hedegaard (1996) reported a fossil pectinodontine from Late Oligocene concretions of Washington State, United States of America, and diagnosed the shell microstructures of *Pectinodonta*.

Lindberg (1988a) proposed the Pectinodontinae as the sister group of *Acmaea mitra*, Acmaeinae, based on shell structure and radular characters. This latter clade was unknown in Australia until 10 years ago when Marshall (1985) first reported pectinodontine species from New South Wales. Marshall's (1985) description of *Pectinodonta aupouria*, *P. morioria* and *P. kapalae* (Fig. 15.37) represented the first report of pectinodontine species from the austral region, although it is likely that Powell (1979) mistakenly identified *P. aupouria* as the lepetid *Maoricrater explorata*.

Pectinodontine species are found worldwide, at bathymetric ranges from about 300–6000 m. The highest species diversity is centred in the equatorial region with decreasing diversity in the temperate regions. They first appear in the Oligocene of North America (Lindberg & Hedegaard 1996) and are also known from the Miocene of New Zealand (Marshall 1985).

Family Lepetidae

Members of the Lepetidae are diagnosed by the fusion of the inner lateral teeth, the loss of the outer lateral tooth field, ctenidium, osphradial ganglia and osphradia, and the reduction of mantle tentacles (Fig. 15.33E, F). They also have only a single pair of salivary glands and the eyes lack pigment (Angerer & Haszprunar 1996). The shells are typically white with little sculpture. Radial and cancellate sculptures are common, but some concentric sculpture (*i.e.* only growth lines) occur in some species. The apex is anteriorly situated. Lepetids have a unique pair of sensory streaks along the antero-lateral surface of the mantle (Angerer & Haszprunar 1996). Each radular tooth row consists of a fused inner lateral tooth flanked by a second pair of inner laterals, often reduced in size, and two pairs of large uncini which can be frilled; the outer lateral tooth field is absent (Fig. 15.34F).

Lepetids are strictly subtidal. They can occur just below the low water mark in the Northern Hemisphere, but submerge to depths in excess of 5000 m towards the equator (Moskalev 1977). Unlike other patellogastropods they do not appear to feed on algae. Instead, detrital material appears to be a major component of their diet, at least for those in shallower waters (Yonge 1960b).

Lepetids occur primarily in the Northern Hemisphere. There are at least six widely distributed taxa in the North Pacific and North Atlantic Oceans, but only two species occur in the Southern Hemisphere. One of these is *Maoricrater explorata* which is found in the vicinity of Australia (New Zealand and Subantarctic waters) – there are no confirmed reports from continental waters. Fossil occurrences of lepetid species date only from the Pliocene of North America and Europe. The relationships of the Lepetidae to other acmaeoidean taxa is problematic. This taxon has a plethora of unique character states. Although these are valuable for identifying lepetids they are useless for inference of relationships. Lindberg & Hedegaard (1996) have argued that the Lepetidae are more closely related to the Lottiidae than the Acmaeidae. They based their argument on the fact lepetids are grouped within the Acmaeidae primarily on the basis of shell characters, whereas the features that group them with the Lottiidae are the more conservative shell microstructure and anatomical characters. They therefore place greater weight on these latter characters. Alternatively, Lepetidae are the sister taxon of the unnamed clade that includes both the Acmaeidae and Lottiidae (Fig. 15.31). The subfamily Propilidiinae is recorded from Australian waters.

Subfamily Propilidiinae

Members of the subfamily Propilidiinae are distinguished primarily by shell features. They are the only patellogastropods with a posteriorly directed apex and an internal septum, but are

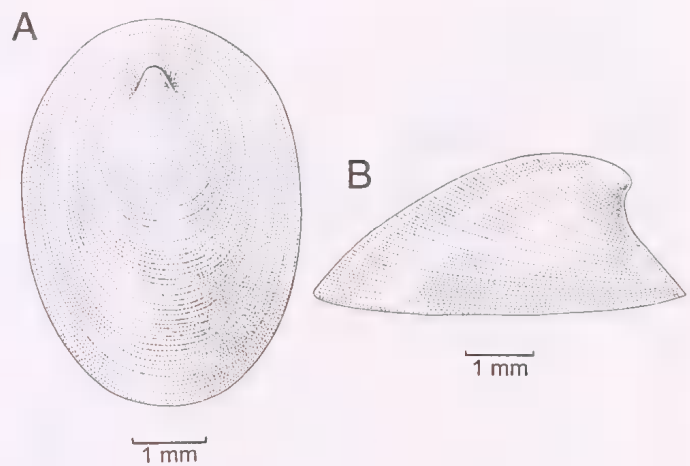


Figure 15.38 Family Lepetidae, subfamily Propilidiinae. *Propilidium tasmanicum*, shell: A, dorsal view; B, lateral view. [R. Plant]

included in Lepetidae on the grounds that they share anatomical characters states and, particularly, have sensory streaks on the mantle (Angerer & Haszprunar 1996). The shell structure differs from that of other lepetids, the innermost layer resembling the coiled fibre layer described by Carter & Clark (1985). The propilidine radula (Fig. 15.34F) resembles that of other lepetids.

Propilidine species are found in both the Northern and Southern Hemisphere. Species diversity is low with single species in the North Pacific (*Propilidium teramachii*), North Atlantic Ocean and Mediterranean (*P. ancyloides*), one species in the Antarctic (*P. pelseneeri*), and a single species in temperate eastern Australia (*P. tasmanicum*, Fig. 15.38). A possible fifth species occurs in the Galapagos Islands (J.H. McLean personal communication). Fossils of *Propilidium* species have been reported from the Neogene of the Europe (Jeffreys 1883; Keen 1960a).

Marshall (1986) was the first to recognise the Australian member of this group. Although *Propilidium tasmanicum* was originally described as a patellogastropod, Hedley (1903) allocated it to *Cocculina* where it remained until Marshall's study. Unlike other propilidines the Australian species is remarkably abundant and large numbers of shells often occur in bottom samples. Nevertheless, only one living specimen has ever been found: May (1923) reported *P. tasmanicum* from algal holdfasts. The evolutionary relationship between this Australian species and its North Atlantic congeners is uncertain.

Family Lottiidae

Although this group is the most diverse and abundant of all patellogastropod families, it is diagnosed by few characters, and perhaps most notably by the loss of calcitic foliated shell structures. Foliated shell structures are present in the Patelloidea, Nacelloidea and many Acmaeoidea, but are absent in the Lottiidae (Fig. 15.32). The remaining anatomical and shell characters of the Lottiidae are all found in different combinations in one or more of the outgroups. Two subfamilies, Lottiinae and Patelloidinae, have been recognised based on radular and shell microstructure characters; both are represented in the Australian fauna.

In Australia, as well as North America, Japan and South America, the vast majority of the species in the nearshore patellogastropod guilds are members of this family. Unlike acmaeoideans, lottiid species are not found in the deep sea. Instead they are primarily intertidal and rarely occur deeper than 30 m. They occupy a wide range of intertidal heights and habitat types. Some species are tolerant of brackish water and can be found in estuarine habitats; others are associated with algae and marine angiosperms; and yet others are found only on carbonate substrata.

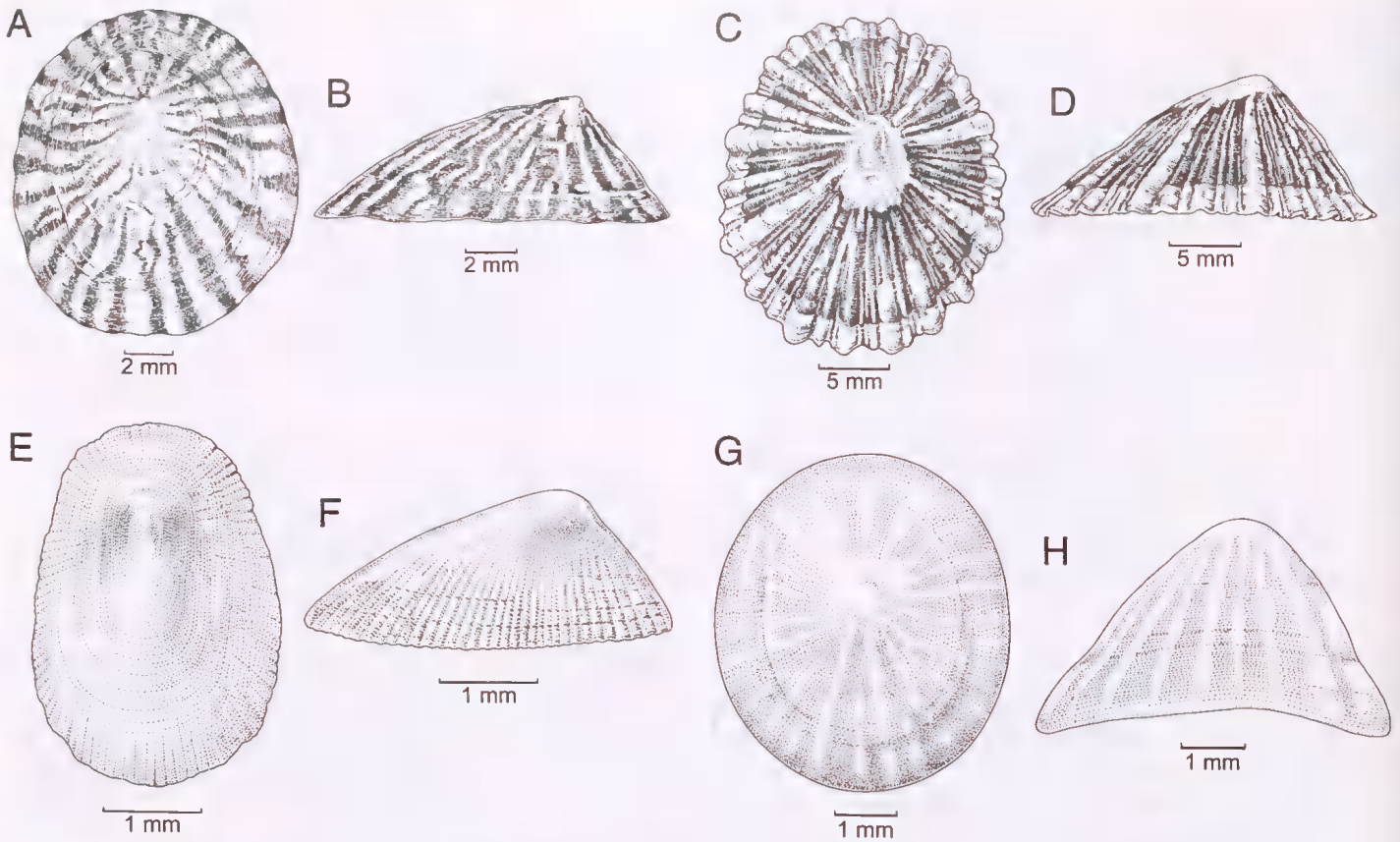


Figure 15.39 Family Lottiidae, subfamily Lottinae. Shells of Australian species: A, B, *Notoacmea petterdi*; C, D, *Lottia onychitis*; E, F, *Asteracmea stowae*; G, H, *Asteracmea axiaerata*. A, C, E, G, dorsal views; B, D, F, H, lateral views. [R. Plant]

Many intertidal groups are speciose; in Australia alone there are at least 25 lottiid species (Ponder & Creese 1980; Lindberg unpublished data). Like patelloidean taxa, these species have figured prominently in studies of rocky shores (Underwood 1975b, 1976a, 1976b; Black 1977; Creese 1980a, 1982; Mapstone *et al.* 1984; Jernakoff 1985a, 1985b; Fletcher 1987, 1988a, 1988b; Black, Lymbery & Hill 1988; Wells & Keesing 1988; Kohn 1993; Yipp 1993).

Lottiids are distributed worldwide with the exception of Antarctica. There are no strong biogeographical trends in the global distribution of lottiids, and different taxa in a single clade may range from cool temperate to tropical environs. The Lottiidae can be identified in the Cretaceous on the basis of shell microstructure and radular characters (Akpan, Farrow & Morris 1982; Lindberg 1988a). By the Eocene, circulatory characters that diagnose living taxa are visible as impressions preserved on the interior of fossil shells (Lindberg & Squires 1990).

Subfamily Lottiinae

It is impossible to distinguish members of the Lottiinae from the Patelloidinae by gross shell characters alone. The few heavily ribbed lottiine species in Australia allow one to exclude species from this subfamily, but there are no diagnostic shell characters by which to include taxa. Instead, they are diagnosed on shell microstructure and radular features, and mantle tentacle configurations.

The fossil distribution of the lottiine species suggests a North Pacific origin for the group with subsequent migration into the North Atlantic, Caribbean and South America, and along the western margin into the Southern Hemisphere and Australia. The group is especially well developed in the north-eastern Pacific (Lindberg 1986b). Fossil members of the taxon are known from the Pliocene and Pleistocene of Japan, North and South America and Europe. Only Pleistocene taxa are known from Australia (Valentine 1965; Lindberg unpublished data).

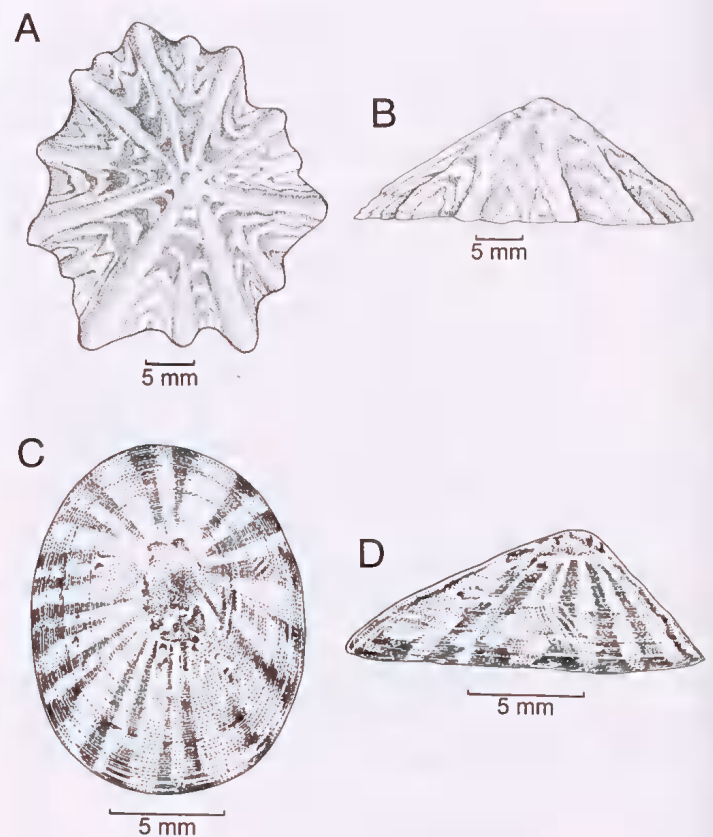


Figure 15.40 Family Lottiidae, subfamily Patelloidinae. Shells of Australian species: A, B, *Patelloida saccharina*; C, D, *Patelloida mimula*. A, C, dorsal views; B, D, lateral views. [A, B, S. Weidland; C, D, R. Plant]

Lottiine species are broadly distributed throughout southern coastal Australia; there are no species known from north of 20°S latitude. They are more diverse in the higher intertidal and on exposed shores than they are at lower levels and in protected habitats (Fig. 15.41; Table 15.3). Ponder & Creese (1980) have provided the most complete treatment of this group.

Australian lottiine species have been described in the genera *Collisella* and *Notoacmea*, and all are endemic. *Collisella* is now recognised as synonym of *Lottia*. The presence of *Lottia* species in Australia, however, is problematic. *Lottia* is a large and diverse genus, ranging from Japan to Chile along the Pacific margin. The Australian species are clearly outliers and whether or not they share common ancestry with other *Lottia* species has not been demonstrated. Alternatively, they could represent an independent derivation from an Australian patelloidine-like common ancestor. There are at least three *Lottia* species in Australia – *L. mixta*, *L. onychitis* (Fig. 15.39C, D), and one undescribed species (Lindberg unpublished data).

Australian *Notoacmea* species are also all endemic although members of this genus are thought to occur in New Zealand (MacClintock 1967; Lindberg 1988a). The use of this genus by North American workers (Fritchman 1960; McLean 1966) for non-Australasian taxa was unfortunate and erroneous as this clade appears to be restricted to Australia and New Zealand (Lindberg 1986b, 1988a). Species of *Notoacmea* lack uncini. There are more than six species of *Notoacmea* in Australia: *N. alta*, *N. conoidea*, *N. corrodena*, *N. flammea*, *N. mayi* and *N. petterdi* (Fig. 15.39A, B), and an undescribed species in northern Australia (Lindberg unpublished data).

Species in the *Asteracmea* group of lottiines are small-shelled and are commonly found in beach drift and amongst algal washings. Some *Asteracmea* species have been reported to be associated with seagrasses (Cotton 1959a), and the distinctive shell morphology of parallel lateral shell margins is present in *Asteracmea stowae* (Fig. 15.39E, F). This group is currently under study by Lindberg; its relationship with either the patelloidines or lottiines is presently unclear. Whereas some members of this group appear to be endemic to Australia (for example, *A. illibrata* and *A. crebristriata*), specimens that appear to be identical to *A. stowae* (Fig. 15.39E, F) and *A. axiaerata* (Fig. 15.39G, H) are present in sediment and coral rubble samples from as far away as the Red Sea and the Caribbean. The most comprehensive study of a member of this taxon is that of Sasaki & Okutani (1993b) on *Yayoiacmea oyamai*; the Japanese species is associated with coralline algae. The small size (typically less than 5 mm in length) of these species undoubtedly contributes to the paucity of knowledge regarding their distribution and habits.

Subfamily Patelloidinae

Patelloidinae are distinguished from other lottiid taxa by shell structure and radular character differences. In comparison with lottiines, patelloidine species lack well-developed exterior homogeneous shell microstructures (Hedegaard 1990). The primitive character state for patelloidines is possession of two pairs of uncini (Fig. 15.34G) (for lottiines, a single pair of uncini, Fig. 15.34H). Subsequent specialisation has involved complete loss of uncini in both subfamilies (Fig. 15.34I).

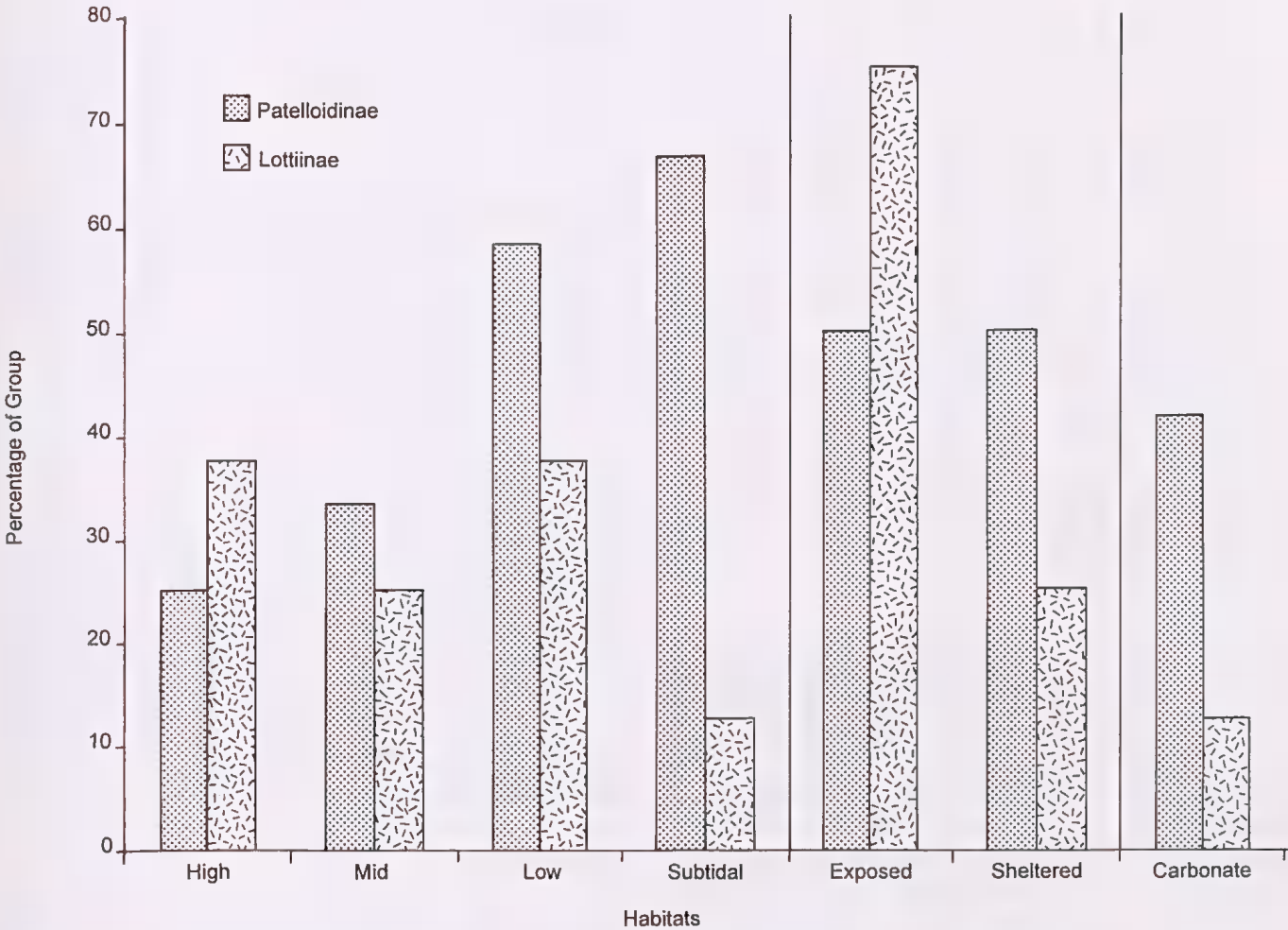


Figure 15.41 Distributions of Australian Patelloidinae and Lottiinae species by (1) intertidal height (high, mid, low and subtidal categories), (2) degree of wave exposure (exposed and sheltered categories), and (3) association with carbonate substrata (carbonate category). Data from Ponder & Creese (1980); see Table 15.3. [C. Eadie]

15. PROSOBRANCHS

Table 15.3 Habitat characteristics of Australian Lottiidae. (After Ponder & Creese 1980)

Taxon	High	Mid	Low	Subtidal	Exposed	Sheltered	Carbonate
Patelloidinae							
<i>Patelloida alticostata</i>			◆	◆	◆		◆
<i>Patelloida belatulla</i>				◆		◆	◆
<i>Patelloida cryptalirata</i>	◆	◆	◆			◆	
<i>Patelloida heteromorpha</i>	◆	◆				◆	
<i>Patelloida insignis</i>			◆	◆		◆	
<i>Patelloida latistrigata</i>	◆	◆			◆		
<i>Patelloida mimula</i>			◆	◆		◆	◆
<i>Patelloida mufia</i>			◆	◆		◆	◆
<i>Patelloida nigrosulcata</i>			◆	◆	◆		◆
<i>Patelloida calamus</i>				◆	◆		
<i>Patelloida saccharina</i>		◆	◆		◆		
<i>Patelloida victoriana</i>				◆	◆		
Lottiinae							
<i>Notoacmea alta</i>		◆			◆		◆
<i>Notoacmea conoidea</i>				◆		◆	
<i>Notoacmea corrodenda</i>			◆		◆		
<i>Notoacmea flammea</i>			◆			◆	
<i>Notoacmea mayi</i>	◆				◆		
<i>Notoacmea petterdi</i>	◆				◆		
<i>Lottia mixta</i>	◆	◆			◆		
<i>Lottia onychitis</i>			◆		◆		

Shell morphology is virtually useless for distinguishing patelloidine species. Apex position, ribbing, colour, size, etc. provide no characters for discriminating between taxa. However, in the Australian fauna all the heavily ribbed species are members of the Patelloidinae (Fig. 15.40A, B), whereas there are few heavily ribbed lottiine species in the fauna (Fig. 15.39C, D). Unfortunately both groups are represented in the fauna by numerous smooth and lightly ribbed taxa (Figs 15.39A, B, 15.40C, D). Ponder & Creese (1980) have provided the most complete treatment of this group.

The Patelloidinae are probably the oldest and most primitive of the lottiids. This thesis is based on the radular and shell structure characters discussed above as well as the fossil record. The taxon was first proposed at the family rank by Oliver (1926). No reference to earlier family names (Lottiidae, Acmaeidae or Tecturidae) was made and it is unclear why Oliver proposed the then synonymous Patelloididae. Golikov & Kussakin (1972) reduced Patelloididae to subfamily rank, defining the taxon on shell, radular and snout characters, and referring *Collisella*, *Notoacmea*, *Testudinalia* and *Patelloida* to the group. This classification was not adopted by subsequent workers (Christiaens 1975a, 1975b; Ponder & Creese 1980; Lindberg 1981c, 1983, 1988a).

The present global distribution of the Patelloidinae strongly suggests a Tethyan origin: members of the group occur from the east coast of Africa through the Indian Ocean, the Australasian region, the tropical western, central, and eastern Pacific, and the Caribbean. The group is especially well developed in the western Pacific including Australia. Fossil patelloidines are known from the Cretaceous, Palaeocene, and Eocene of California, the Cretaceous of England, the Eocene of France, the Eocene of Oregon, and the Oligocene of Washington and British Columbia, Canada (Lindberg & Vermeij 1985) and the Miocene of Australia (Chapman & Gabriel 1923).

Patelloidine species are broadly distributed throughout coastal Australia, with about equal species diversity in both temperate and tropical Australia. This is in marked contrast with Australian

Lottiinae. Patelloidinae also tend to be more diverse in the lower intertidal, on sheltered shores, and in association with carbonate substrata (Fig. 15.41; Table 15.3). These simple patterns suggest that historical factors are likely to play a role in the ecology of Australian Lottiidae and therefore caution must be adopted when conducting surveys and studies that require, or are based on, assumptions and generalisations about 'limpets'.

All Australian patelloidines are currently assigned to the genus *Patelloida* and are endemic with the sole exception of *Patelloida saccharina* (Fig. 15.40A, B) which extends northward into the Indo-West Pacific. The endemic Australian species include: *P. alticostata*, *P. bellatula*, *P. cryptalirata*, *P. heteromorpha*, *P. insignis*, *P. latistrigata*, *P. mimula* (Fig. 15.40C, D), *P. mufria*, *P. nigrosulcata*, *P. calamus* and *P. victoriana*.

Subclass ORTHOGASTROPODA

The Orthogastropoda (Ponder & Lindberg 1996) includes all gastropods other than the Eogastropoda. Members of this clade are distinguished from eogastropods by having a flexoglossate radula, a hypobranchial gland, a propodium, paired jaws (in most members), statocysts anterior or dorsal to the pedal ganglia and showing significant reduction in the extent of the pallial nerves.

The development of the flexoglossate radula (Salvini-Plawen 1988) was a major innovation in gastropod evolution (Golikov & Starobogatov 1975). Its unique longitudinal bending plane enabled the radular teeth to adopt an array of new functions, particularly allowing the marginal teeth to sweep inwards. The stereoglossate radula functions like a rasp on a hard substratum, whereas the flexoglossate condition allows the radulae to function as shears, brooms and knives (Ankel 1936a; Hickman & Morris 1985).

Four major monophyletic groups are now recognised among the Orthogastropoda: Vetigastropoda, Neritopsina, Caenogastropoda and Heterobranchia. Cocculinoidea and some of the hot-vent taxa form smaller, currently less well-resolved, groups (Ponder & Lindberg 1997).

Superorder COCCULINIFORMIA

The Cocculiniformia is currently classified as an order or suborder of the streptoneurous Gastropoda. The taxon contains about 130 Recent marine species. Despite the small number of taxa, the group is very diverse anatomically and biologically. This diversity is reflected in the recognition of two superfamilies and ten families within the group. Members of the Cocculiniformia are found worldwide and live predominantly on biogenic substrata in deeper waters down to the hadal zone. One pseudococculinid species and one family, the Pyropeltidae, are known from the hydrothermal-vent habitat.

Early works on the taxonomy and anatomy of the cocculiniform gastropods were provided by Verrill (1880, 1881a, 1882, 1884), Dall (1882, 1889), Pelseneer (1900) and Thiele (1903, 1908, 1909). Some 60 years later, modern research started with a series of taxonomic papers by Moskalev (1971, 1973, 1976, 1978), some biological notes by Italian workers (Panetta 1973; Villa 1983; Bogi 1984; Ragozzi 1985; Gubbioli & Nofroni 1986) and a review of radulae and feeding biology by Hickman (1983, 1984c). Taxonomic papers using scanning electron microscopical techniques followed and include works by Marshall (1983a, 1986, 1987, 1994, 1996), McLean (1985, 1987, 1988c, 1991, 1992a, 1992b), McLean & Haszprunar (1987), Warén (1993), Dantart & Luque (1994), McLean & Harasewych (1995), Haszprunar & McLean (1996) and Warén & Gofas (1996). Detailed anatomical information and phylogenetic considerations are provided by Haszprunar (1987a, 1987c, 1988a, 1988c, 1988d, 1988e, 1992a) and Haszprunar & McLean (1996).

The group is highly diverse and thus it is difficult to diagnose the Cocculiniformia as a whole, although each family is readily diagnosed by distinct shell and radular characters. In addition, the monophyly of the group is not yet fully confirmed, and a dual origin of the two main subgroups has been suggested by Ponder & Lindberg (1996), with possible neritimorph affinities of Cocculinoidea, and vetigastropod affinities of Lepetelloidea. Basic synapomorphies are found in the shared functional overlapping of marginal teeth (Figs 15.42C, 15.48A; Hickman 1983), the common pattern of the oesophageal folds (Salvini-Plawen & Haszprunar 1987), and in the fact that the gill is situated in the shallow mantle cavity at the right side (Figs 15.42G, 15.43E, 15.50A–G) and yet is innervated from the left side.

In general, cocculiniform gastropods may be characterised as follows. Like the Patellogastropoda most Cocculiniformia have no trace of coiling even in the juvenile teleoconch, and are termed symmetrical limpets. In some species the periostracum forms distinct patterns (Figs 15.43A, B, 15.45E, F). The shell shape usually is patelliform, the position of the apex varies between central and posterior, and the apex itself may be strongly eroded. Certain species, such as *Cocculina pristina*, *Cocculina baxteri* and all addisoniids (Fig. 15.45P, Q; see McLean 1985; Dantart & Luque 1994), become asymmetrical as adults in that the apex is more or less deflected to the left; in *Xenodonta bogasoni* the apex is slightly deflected to the right (Warén 1993). Choristellids have a helicoid teleoconch (Fig. 15.45N). The bilaterally symmetrical embryonic shell (protoconch I; Fig. 15.45H) often forms a distinct angle with the teleoconch (Fig. 15.45F); a larval shell (protoconch II) is lacking. The shell is usually very fragile and thin, with weak sculpture, and is generally white in colour. The shell structure has not yet been studied extensively (for example, Hedegaard 1990), but in general, crossed-lamellar aragonite is present, whereas nacre is lacking.

The head bears a single pair of tentacles, the right one of which is often used as a copulatory organ (Figs 15.42D, 15.46F–H). In certain cocculinids and all bathysciadiids a copulatory organ proper is present beneath the right cephalic tentacle (Figs 15.42E, 15.43D). An open seminal groove along the right side of the neck transports the sperm from the genital opening on the right side of

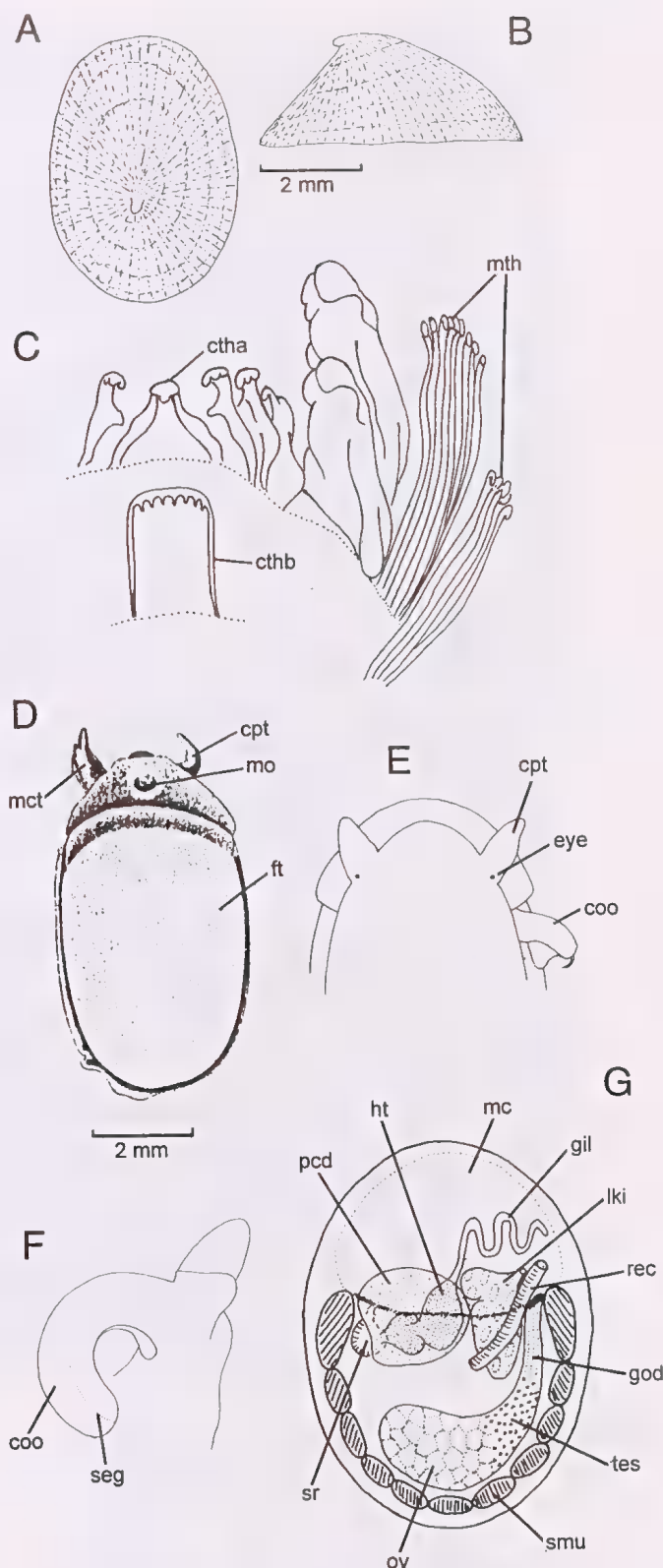


Figure 15.42 Family Cocculinidae. A, B, *Coccopigya hispida*, shell: A, dorsal view; B, lateral view, right side. C, representative cocculinid radula section, showing two examples of central teeth (ctha, cthb) and the overlapping functional row of marginal teeth. D, *Coccocrater radiata*, ventral view of animal showing the modified right cephalic tentacle which is used as a copulatory organ. E, *Paracocculina cervae*, head, dorsal view, showing copulatory organ, cephalic tentacles and reduced eyes. F, *Coccopigya hispida*, dorsal view of modified right cephalic tentacle with copulatory organ. G, semischematic diagram of shell muscle, mantle cavity and gonopercardial system, viewed dorsally. coo, copulatory organ; cpt, cephalic tentacle; ctha, cthb, central teeth, two examples, a and b; eye, eye; ft, foot; gil, gill; god, gonoduct; ht, heart; lki, left kidney; mc, mantle cavity; mct, modified cephalic tentacle; mo, mouth; mth, marginal teeth; ov, ovary; pcd, pericardium; rec, rectum; seg, seminal groove; smu, shell muscle; sr, seminal receptacle; tes, testis. (A, B, E, F, after Marshall 1986; C, after scanning electron micrographs of Hickman 1984c and McLean 1987; D, after Thiele 1903; G, modified after Haszprunar 1988a) [G. Haszprunar]

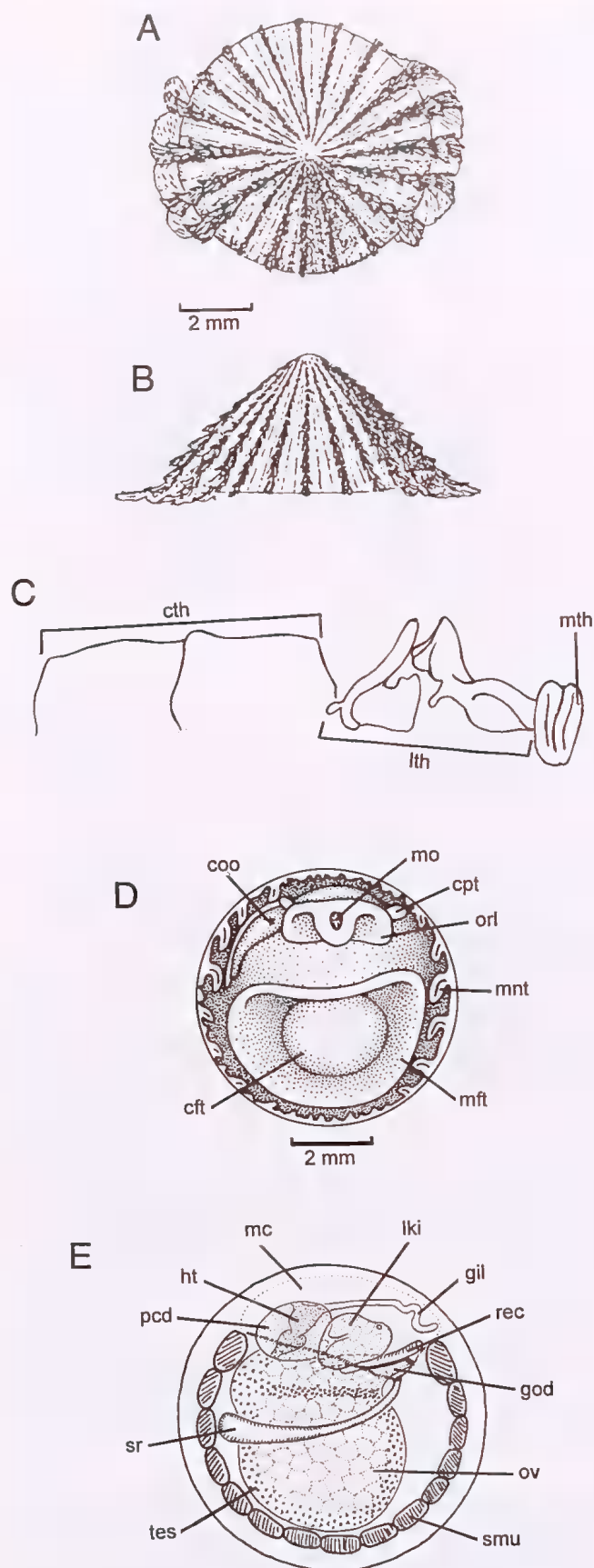


Figure 15.43 Family Bathysciadiidae. A, B, *Bathypelta pacificum*, shell: A, dorsal view; B, anterior view. C, *Bathysciadium* sp., section of modified radula. D, *Bathypelta pacificum*, animal, ventral view, showing head, foot (pedal disk) and copulatory organ at right side. E, *Bathysciadium conicum*, semischematic diagram of shell muscle, mantle cavity and gonopercardial system, dorsal view. cft, central region of foot; coo, copulatory organ; cpt, cephalic tentacle; cth, central tooth; gil, gill; god, gonoduct; ht, heart; lki, left kidney; lth, lateral teeth; mc, mantle cavity; mft, marginal region of foot; mnt, mantle tentacle; mo, mouth; mth, marginal teeth; orl, oral lappet; ov, ovary; pcd, pericardium; rec, rectum; smu, shell muscle; sr, seminal receptacle; tes, testis. (A, B, after Dall 1908; C, after scanning electron micrographs of Warén 1993; D, after Thiele 1908; E, after Haszprunar unpublished data) [G. Haszprunar]

the mantle cavity to the base of the copulatory organ. Oral lappets are present in several families (Figs 15.43D, 15.46C, E), but lacking in others (Fig. 15.46A, D). The eyes are more or less reduced and sometimes absent. The sole of the foot (= pedal disk) is usually divided into a central and marginal region (Figs 15.43D, 15.46C, E) (which is not always visible from an external view) and the pedal gland is often reduced or lost in adults. A single pair of epipodial tentacles is usually present in most Cocculiniformia, but some species of the Choristellidae have several pairs, certain Lepetellidae show a single, terminal one, and the tentacles are absent in some taxa (*Coccapigya*, Bathysciadiidae, Cocculinellidae, Addisoniidae). An operculum is lacking in all adults except for members of the Choristellidae.

The mantle cavity is very shallow (that is, it is a nuchal cavity; Fig. 15.50A, D–G) except in Lepetellidae (Fig. 15.50B, C) and Choristellidae (Fig. 15.50H). The gills, which may be secondary structures (Haszprunar 1988d), are variable and range from a series of small ciliary tufts to large, complex organs composed of leaflets (Lepetelloidea) or form a single fold (Cocculinoidea). The mantle margin is often very wide and is provided with an extensive supply of blood sinuses. It probably plays an important role in respiration. The heart is generally monotocardian, and one or two kidneys are present. With the exception of the Choristellidae, all cocculiniforms are hermaphrodites. True internal, or ent-aquatic, fertilisation of the large, yolky eggs via copulatory organs occurs in the mantle cavity. All taxa have lecithotrophic development, and brooding of the fertilised eggs in the mantle or subpallial cavity surrounding the shell muscle has been reported for several species (*Coccapigya hispida*, *Notocrater ponderi*, *Lepetella* and *Bathypheophilus* species; see Warén 1972; Moskalev 1978; Haszprunar 1987a, 1988d; Dantart & Luque 1994; Haszprunar & McLean 1996).

Jaws may be paired, fused or lacking, and a subradular organ is generally absent. The basic cocculiniform radula is of the rhipidoglossate type, but in many of the families there is considerable modification of this basic type (Figs 15.43C, 15.48D–H). In general, cocculiniform gastropods feed on the biogenic substratum on which they live. Their mode of feeding is not known in detail, but they may glean decaying bacteria from the substratum or eat the substratum itself, either assisted by symbiotic bacteria or by using their own enzymes. Accordingly, the alimentary tract is often greatly modified and specialised (Fig. 15.49) with respect to size and form of the oesophageal glands (pouches or tubes), the stomach (very large, small, vestigial or absent), the digestive gland (midgut gland – with one, two or several openings or none), the intestine (huge sac, very thin, many loops or short) and the rectum (passing or penetrating the heart).

Thus, the Cocculiniformia as a whole represents a remarkable example of adaptive radiation in various deep-water habitats mainly by exploiting organic material for nourishment. Although cocculiniform gastropods do not have any commercial or economic importance, they probably play a significant role in the breakdown of biogenic material in deeper waters (Wolff 1976, 1979). Crustacean parasites have been reported for certain species (see Jones & Marshall 1986; Haszprunar 1987a).

Probably because of their deep-sea habitat and their thin and fragile shells, the current fossil record of undoubted Cocculiniformia only dates back to the early Tertiary (Marshall 1986). However, based on features of their anatomy, it appears almost certain that the group had its origin in the early Palaeozoic. The Cocculiniformia are clearly divided into two superfamilies, the Cocculinoidea and the Lepetelloidea. Both superfamilies are represented in Australian and New Zealand waters. Since many genera are found worldwide, taxa recorded from the New Zealand region are included here as they will almost certainly be found in Australian waters.

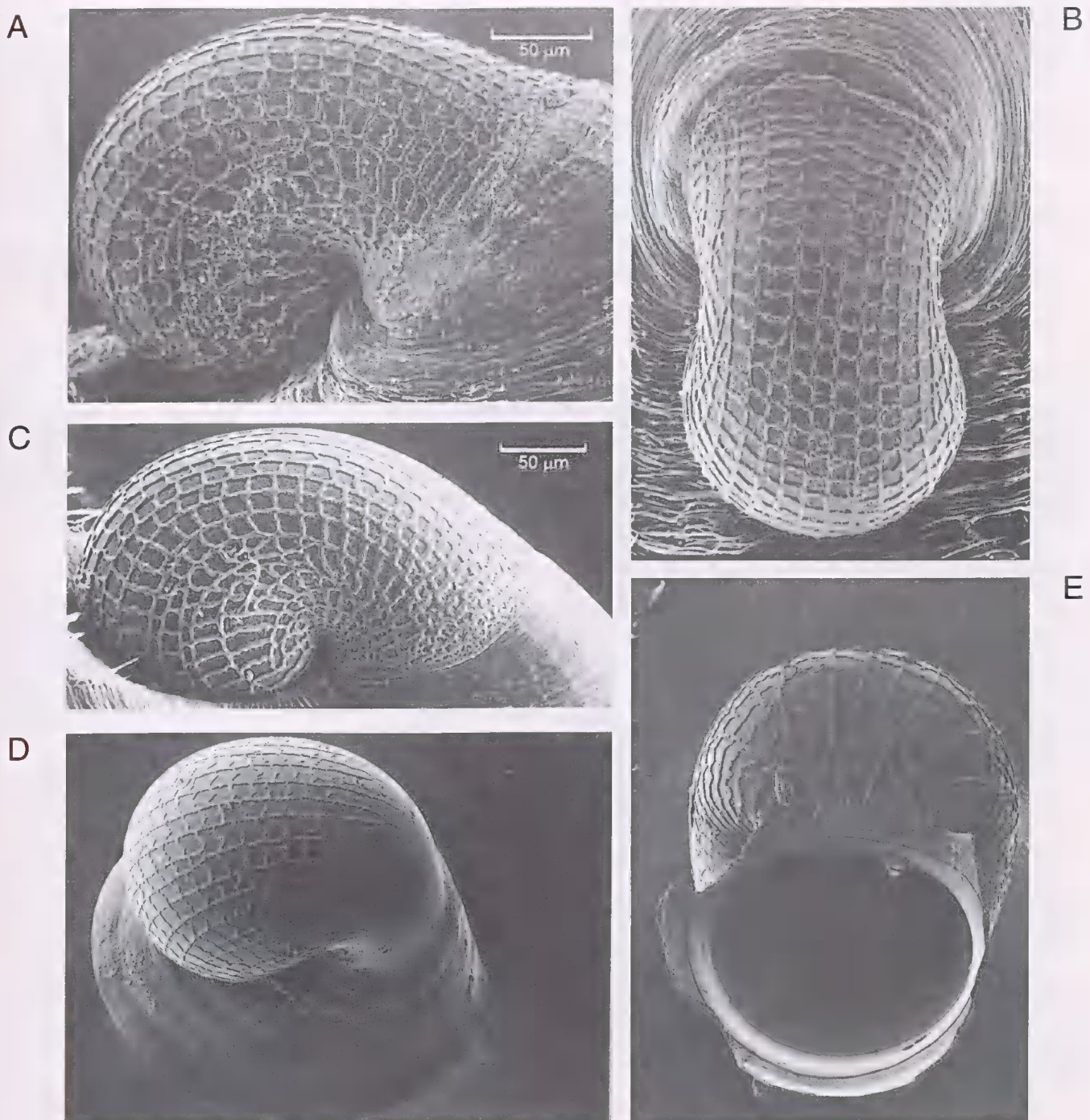


Figure 15.44 Superfamily Cocculinoidea. Protoconchs. A–C, family Cocculinidae: A, B, *Coccopigya spinigera*, right side view (A), and dorsal view (B), note the partial fusion with the limpet-like early teleoconch; C, *Coccopigya hispida*, right side view. D, E, family Bathysciadiidae, *Bathysciadium* aff. *costulatum*: D, right dorsal view including part of teleoconch, note the juvenile limpet condition (protoconch length = 450 µm); E, ventral view. [A, B, D, E, A. Warén; C, B. Marshall]

Superfamily COCCULINOIDEA

The Cocculinoidea is a small group of symmetrical limpets; most species are placed in the family Cocculinidae. They are found worldwide in deeper waters (from 30 m to abyssal depths) and are predominant in the deep sea.

Cocculinoideans differ from the Lepetelloidea in having a protoconch with a free tip and shell muscle that is always composed of several distinct bundles. The central tooth is weakly developed, vestigial or even absent, and there is always a single pair of radular cartilages.

The patelliform shell has an oval to circular aperture and the periostracum may have specific structures such as spines or lappets. The shell-muscles form several distinct bundles and the shell-muscle scar is horseshoe-shaped (Figs 15.42G, 15.43E). Oral lappets are generally present. A copulatory organ may be situated

on or behind the right cephalic tentacle (Figs 15.42E, F, 15.43D), or the right cephalic tentacle may be modified to act as a copulatory organ (Fig. 15.42D). Eyes are either reduced or absent. A single pair of epipodial tentacles may be present or absent. Adults lack an operculum.

The shallow mantle cavity contains a prominent gill of the pseudoplicate type, which closely resembles those of bullomorph opisthobranchs in consisting of a single, meandering fold (Thiele 1908; Haszprunar 1987a). A hypobranchial gland is present. The large heart is monotocardian, and only the left kidney is present (Figs 15.42G, 15.43E). All cocculinoideans have a truly hermaphroditic gland, and a single, glandular gonoduct. Sperm are transferred via the copulatory organ and are stored in one or two receptacula. Fertilisation probably occurs in the glandular gonoduct, which opens into the right posterior end of the mantle cavity.

15. PROSOBRANCHS

Within the Cocculinoidea there is a trend from the rhipidoglossate type of radula in the Cocculinidae to a greatly modified type in the Bathysciadiidae (Figs 15.42C, 15.43C). This parallels to some extent a shift from wood to (dead) cephalopod beaks as ■ substratum and food. *Teuthirostria cancellata* from off northern Peru combines the cocculinid anatomy (G. Haszprunar personal observation) with the bathysciadiid substratum. Jaws are vestigial or lacking.

All Cocculinoidea are characterised by true pedal ganglia and by statocysts containing a single, concentrically structured statolith (Thiele 1908; Haszprunar 1987a).

The superfamily presently comprises the families Cocculinidae and Bathysciadiidae, both of which are represented in the Australian–New Zealand area.

Family Cocculinidae

The Cocculinidae are a cosmopolitan family, comprising at least 30 extant species. They are found from depths of 30 m to more than 3700 m. Most species feed on decaying wood, but certain species live on cephalopod beaks (*Teuthirostria cancellata*; Moskalev 1976) or on whale bone (*Cocculina craigsmithi*; McLean 1992b).

Six nominal genera are included in the Cocculinidae: *Cocculina*, *Fedikovella*, *Teuthirostria*, *Coccapigya*, *Paracocculina*, and *Coccocrater*. These can be distinguished on features of the shell, radula, external morphology, and internal anatomy. The extant Australian and New Zealand fauna consists of *Coccapigya barbatula* from New South Wales and *C. crenilamina*, *C. hispida* (Fig. 15.42A, B, F), *C. oculifera* and *Paracocculina cervae* (Fig. 15.42E) from New Zealand, and *C. crinita* from both New South Wales and New Zealand (see Moskalev 1976; Marshall 1986, 1994; Haszprunar 1987a; McLean 1987).

Cocculinids have an oval aperture, and the typical rhipidoglossate radula is diagnostic for the family (Fig. 15.42C). A single jaw, oesophageal pouches, a single digestive gland, and several intestinal loops characterise the alimentary tract.

The shell is thin and porcellaneous and has radial or concentric sculpture (Fig. 15.42A, B). The apex of the shell is centrally or posteriorly situated, and its height is variable. The protoconch is usually retained in the adult, has a free tip and often has a reticulate sculpture (Fig. 15.44A–C). The external morphology is as described for the superfamily. The genus *Coccapigya* is characterised by a spinose periostracum and by the lack of epipodial tentacles.

The subpallial cavity, which surrounds the shell muscle, bears a more or less prominent 'subpallial' gland. The pallial hypobranchial gland is quite variable in size and forms a brood pouch in many species. The shallow mantle cavity always contains a pseudoplicate gill (Thiele 1903; Haszprunar 1987a). The hermaphroditic genital system (Fig. 15.42G) has a glandular gonoduct and one or two distinct receptacula for the storage of sperm.

Cuticular 'hairs' form a basket-like structure of unknown function at the mouth opening. The single jaw-element is small, the sublingual pouch is glandular and the salivary glands form small pouches. A single pair of radular cartilages and a radular caecum are present. The anterior oesophagus has glandular pouches, and the large stomach contains a gastric shield, but lacks a protostyle and a diverticulum. A single digestive gland is present. There are several intestinal loops, and the rectum passes beneath the heart (Fig. 15.42G).

A distinct blood gland of variable size is situated ventrally in the head. The eyes are usually a modified basi-tentacular gland, but *Coccapigya oculifera* has retained true vesicles, and *C. viminensis* shows no evidence of an eye or an optic nerve (G. Haszprunar personal observations).

The fossil history of the Cocculinidae extends back to the Tertiary.

Family Bathysciadiidae

Bathysciadiidae are a small cosmopolitan family of symmetrical limpets. At present about 30 species are known worldwide (A. Warén & B. Marshall personal communication), of which only five are named (Dall 1908; Moskalev 1973; Dautzenberg & Fischer 1990; Warén 1991, 1993). Bathysciadiids are found from 570 m to hadal depths exceeding 9500 m. They appear to feed exclusively on cephalopod beaks, although there are no data for *Xenodonta* species.

Bathysciadiidae comprise four nominal genera: *Bathysciadium*, *Bathypelta*, *Bonus*, and *Xenodonta*; a fifth genus, *Pilus* (type species: *Cocculina conica*) may also belong here (Warén 1991, 1993). Pelseneer's (1900) anatomical description of *Bathysciadium costulatum* contains many errors, whereas Thiele's (1908) description of *Bathypelta pacificum* (Fig. 15.43A, B) can be confirmed (Haszprunar 1988c, unpublished data). Species of *Xenodonta*, *Pilus*, and *Bonus* have not yet been studied anatomically. Confirmation of the status of the recognised genera awaits detailed study of the protoconch and radular characters; also the structure of the copulatory organ (its size, presence of an open seminal ridge versus an internal duct) is useful (Haszprunar unpublished data). Several, undescribed bathysciadiid species are known from Australian (New South Wales) and New Zealand waters (B. Marshall personal communication).

Bathysciadiids are cocculinoidean limpets with an oval or circular shell aperture and often typical periostracal fringes (Fig. 15.43A, B). The unique radula is highly aberrant with a very weak, but broad central tooth and four lateral teeth (Fig. 15.43C; Warén 1993). Paired jaws, large oesophageal glands, very large stomach, lack of digestive gland, and a very thin intestine characterise the alimentary tract.

The conical shell is thin and fragile, and its aperture ranges from 1–10 mm in diameter. The shell is sculptured with radial ribs. The periostracum is very well developed and often forms radially arranged fringe-like outgrowths (Fig. 15.43A, B). The apex is centrally placed in *Bathysciadium*, *Bathypelta* and *Bonus*, whereas in *Xenodonta* and *Pilus* it is situated posteriorly. The protoconch is usually lost in adults, and its surface is covered by fine pits (*Xenodonta*) or by a reticulate sculpture (Fig. 15.44D, E; *Bathysciadium*; cf. Warén 1993). Prominent oral lappets are present (Fig. 15.43D) and act as suckers (B. Marshall personal communication), whereas eyes and epipodial tentacles are lacking. The subpallial cavity is glandular. Behind the right cephalic tentacle, there is a more or less specialised, true copulatory organ.

The shallow mantle cavity contains a pseudoplicate gill in all species investigated anatomically (Thiele 1908; Haszprunar unpublished data). The hermaphroditic genital system has a glandular gonoduct and a distinct seminal receptacle for the storage of sperm (Fig. 15.43E).

Bathysciadiids lack paired jaws, and have a glandular sublingual pouch; the salivary glands form small pouches. A single pair of radular cartilages and a radular caecum are present. The anterior oesophagus gives rise to a pair of large oesophageal glands, that fill most of the body of the animal. The oesophageal glands may functionally replace the digestive glands, which are absent. The very large stomach contains a gastric shield, but lacks a protostyle, style sac and diverticulum. There are few intestinal loops, and the rectum passes beneath the heart.

The nervous system does not show any peculiarities. Epipodial tentacles, osphradium and eyes are always absent, and the statocysts contain a single statolith.

Superfamily LEPETELLOIDEA

Lepetelloidean gastropods are found worldwide in waters ranging in depth from 30 m to the deepest abyssal, but are predominantly found in the deep sea. They are characterised by having a protoconch with a fused tip (Figs 15.45G, 15.47A–E), and shell muscle that is mostly an undivided organ (Fig. 15.50). The central

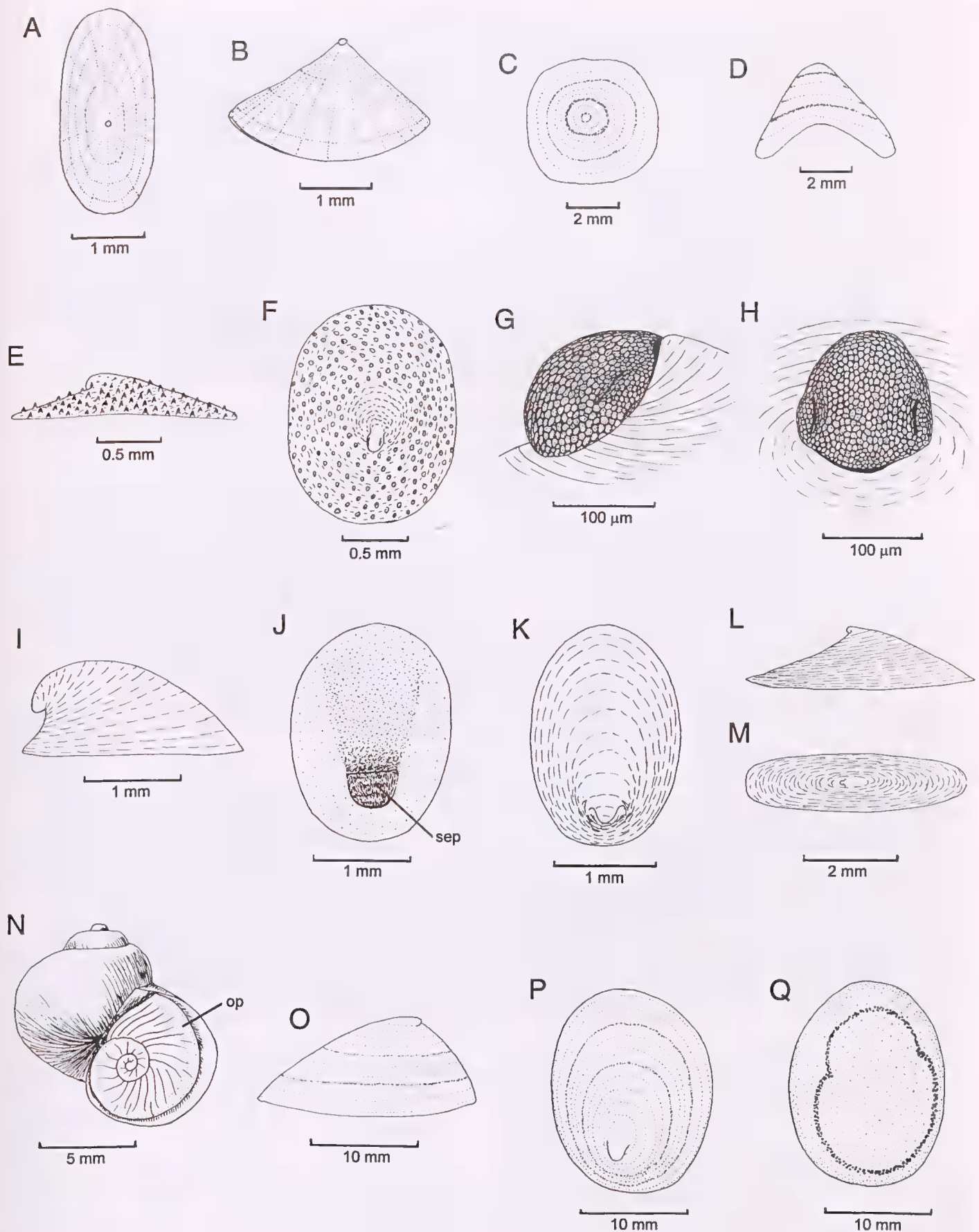


Figure 15.45 Superfamily Lepetelloidea. Shell features. A–D, family Lepetellidae: A, B, *Tectisumen clypidellaeformis*, shell in (A) dorsal view and (B) anterior view; C, D, *Tecticrater compressa*, shell in (C) dorsal view and (D) left lateral view. E, F, family Pseudococculinidae, subfamily Caymanabyssiinae, *Caymanabyssia rhina*, young shell: E, right lateral view; F, dorsal view, note the obliquely orientated protoconch. G–K, family Pseudococculinidae, subfamily Pseudococculininae: G, H, *Mesopelex zelandica*, protoconch with subreticulate sculpture, in (G) right lateral view and (H) dorsal view, showing bilateral symmetry; I–K, *Tentaoculus haptricola*, shell, in (I) lateral view from right side, (J) dorsal view and (K) ventral view showing the septum. L, M, family Cocculinellidae, *Cocculinella coercita*, shell: L, right lateral view; M, dorsal view. N, family Choristellidae, *Choristella tenera*, shell with operculum. O–Q, family Addisoniidae, *Addisonia paradoxa*, shell: O, right lateral view; P, dorsal view; Q, ventral view, showing asymmetry of apex and shell muscle insertions. op, operculum; sep, septum. (A–D, after Suter 1908; E–K, after scanning electron micrographs of Marshall 1986; L, M, combined and modified after Thiele 1909 and Marshall 1986; N, after Verrill 1882; O–Q, combined after Dall 1882 and McLean 1985) [G. Haszprunar]

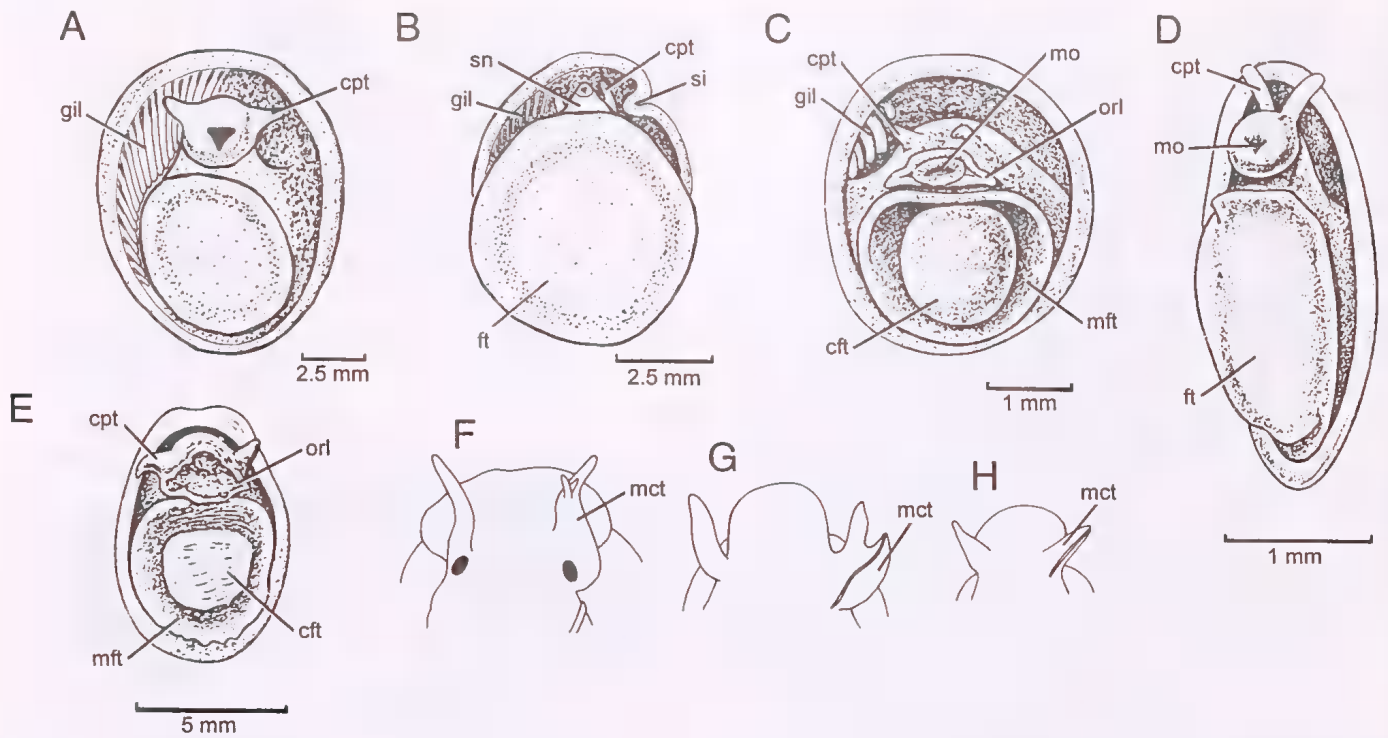


Figure 15.46 Superfamily Lepetelloidea. Features of animals. A, family Addisoniidae, *Addisonia lateralis*, animal, ventral view, showing head, gill filaments and foot (pedal disk). B, family Osteopeltidae, *Osteopelta mirabilis*, animal, ventral view, showing tapered head, mantle siphon at left side, gill filaments and large foot. C, family Lepetellidae, *Lepetella tubicola*, animal, ventral view, showing head with prominent oral lappets, few gill filaments and foot. D, family Cocculinellidae, *Cocculinella minutissima*, animal, ventral view, showing head with oral lappets and tentacles, and foot. E, family Pseudococculinidae, *Pseudococculina concentrica*, animal, ventral view, showing head with oral lappets and tentacles, and foot. F–H, pseudococculinid heads in dorsal view, with copulatory organ: F, *Notocrater craticulata*; G, *Caymanabyssia sinospina*; H, *Colotrachelus hestica*. cft, central portion of foot; cpt, cephalic tentacle; ft, foot (= pedal disk); gil, gill-leaflets; mct, modified right cephalic tentacle to act as a copulatory organ; mft, marginal portion of foot; mo, mouth; orl, oral lappet; si, siphon; sn, snout. (A, B, after Haszprunar 1988; C–E, after Thiele 1909; F–H, after Marshall 1986) [G. Haszprunar]

tooth is well developed. The gill is composed of several tufts or leaflets (Fig. 15.50); a hypobranchial gland is lacking. There are two kidneys, one (or two) simple, ciliated gonoduct(s), and separated testis and ovary (Fig. 15.50A–G). Only the Choristellidae are gonochoristic (Fig. 15.50H). The statocysts contain many statoconia.

Most lepetelloideans are symmetrical limpets, but the shells of adult addisoniids are asymmetrical (Fig. 15.45P), and those of choristellids are coiled with an operculum (Fig. 15.45N). Except in certain lepetellids (Fig. 15.50B), the paired shell-muscle forms a compact horseshoe-shaped organ (Fig. 15.50A, C–G), and choristellids have a single columellar muscle (Fig. 15.50H). Usually the right cephalic tentacle is modified to act as a copulatory organ (Fig. 15.46F–H). Eyes occur in all stages of reduction. The epipodium consists of a single, a pair or several pairs of tentacles.

The shallow mantle cavity contains several gill-leaflets which often continue into the right subpallial cavity (Fig. 15.50F, G). In a number of species, the gill-leaflets are also present on the left mantle roof (Fig. 15.50A). In many families, each leaflet has a distinct pocket, or bursicle, which may have a sensory function. In addisoniids and choristellids, the gill-leaflets are equipped with paired skeletal rods and distinct glandular areas. The heart is monotocardian, and both kidneys are present. The left kidney is situated in the central mantle roof and connected with the pericardium, the right one lies between the viscera and is often connected with the genital system, but never with the pericardium. The gonoducts are never glandular and their number varies among families. Sperm transfer occurs via the copulatory organ, and in some groups sperm are stored in receptacles. Fertilisation may occur in the gonoduct or in the mantle cavity. The details of the lepetelloidean nervous system vary between families.

Jaws may be present or absent, and the salivary glands generally form simple pouches. As in the Cocculinoidea there is a trend from the rhipidoglossate type of radula (Pseudococculinidae,

Pyropeltidae, Osteopeltidae) to fewer teeth (Bathypheophilidae) or greatly modified types (Lepetellidae, Cocculinellidae, Choristellidae, Addisoniidae) (Fig. 15.48A–H). This parallels, to some extent, a shift from wood to other decaying biogenic substrata as a food source.

The superfamily comprises eight families, five of which have been recorded from the Australian area (Lepetellidae, Pseudococculinidae, Osteopeltidae, Cocculinellidae, Choristellidae) and three (Pyropeltidae, Bathypheophilidae, Addisoniidae) which have not. Pyropeltidae (radula Fig. 15.48B; gonopericardial system Fig. 15.50E) are represented by the single genus *Pyropelta* with three species, and are restricted to the hydrothermal-vent habitat or big whale bones, where they feed on bacterial mats (McLean & Haszprunar 1987; McLean 1992b). Bathypheophilidae (radula Fig. 15.48E, mantle cavity and gonopericardial system Fig. 15.50A) include two described species of *Bathypheophilus* and a single species of *Aenigmabonus*. These animals live on rhizomes of seagrass in abyssal depths of the Atlantic and Pacific Ocean (Wolff 1976, 1979; Moskalev 1978; Haszprunar & McLean 1996). Addisoniidae (shell Fig. 15.45O–Q, animal Fig. 15.46A, radula Fig. 15.48F, mantle cavity and gonopericardial system Fig. 15.50G) include four limpet species of *Addisonia* which live in empty egg-cases of sharks and skates (Villa 1983; McLean 1985; Haszprunar 1987c; Simone 1996). The coiled *Helicopelta rostricola* (radula addisoniid-like, no anatomical data) lives on cephalopod beaks (Marshall 1996).

Family Lepetellidae

Lepetellidae are symmetrical limpets with, at present, four nominal genera (*Lepetella*, *Tectisumen*, *Tecticrater* and *Bogia*) and only ten named extant species and several tens of unnamed species (A. Warén personal communication). Only two species have hitherto been reported from the Australian/New Zealand region: *Tectisumen clypidellaeformis* (Fig. 15.45A, B), in 90 m of water, from the Snare Islands off southern New Zealand and



Figure 15.47 Superfamily Lepetelloidea. Protoconchs. **A, B**, family Lepetellidae, *Lepetella* sp.: **A**, right latero-ventral view; **B**, ventral view, showing the nearly perfect symmetry. **C, D**, family Pseudococculinidae: **C**, *Tentaoculus haptricola*, right lateral view; **D**, *Notocrater gracilis*, right lateral view. **E**, family Cocculinellidae, *Cocculinella osteophila*, right lateral view. **F**, family Choristellidae, *Choristella nofronii*, view from above. [A, B, F, A. Warén; C–E, B. Marshall]

Tecticrater compressa (Fig. 15.45C, D) from East Cape, New Zealand (Suter 1908). The remaining species have been described from the Mediterranean and the Atlantic, but the family is probably distributed worldwide. So far as is known all lepetellids feed exclusively on empty tubes of the polychaete genus *Hyalinoecia*.

Lepetellid limpets have a variable, often saddle-like shell. The radula is strongly modified and highly diagnostic (Fig. 15.48D). The alimentary tract is characterised by the lack of jaws, the large oesophageal pouches, and the presence of several openings of the large digestive gland, which are filled by food residues. The testis and ovary are separate, and a common gonoduct leads to a urinogenital chamber and opening (Fig. 15.50B, C).

The thin, porcellaneous shell attains only a few millimetres in size. It usually exhibits weak, concentric sculpture. The shape of the shell aperture depends strongly on the topography of the substratum (Fig. 15.45A–D). The apex is subcentrally placed and is usually eroded in adults; the protoconch shows a reticulate sculpture (Fig. 15.47A, B; Warén 1991). Large oral lappets and eyes may be present (Fig. 15.46C) or absent. Epipodial tentacles are lacking or a single, terminal tentacle is present (Dartart & Luque 1994). A distinct anterior pedal gland is absent and the foot is divided into a non-ciliated central zone and a ciliated marginal zone (Fig. 15.46C). The right cephalic tentacle bears a ciliated seminal groove laterally and acts as a copulatory organ. From its base a seminal groove leads backwards along the right side of the neck to reach the posterior pallial genital opening.

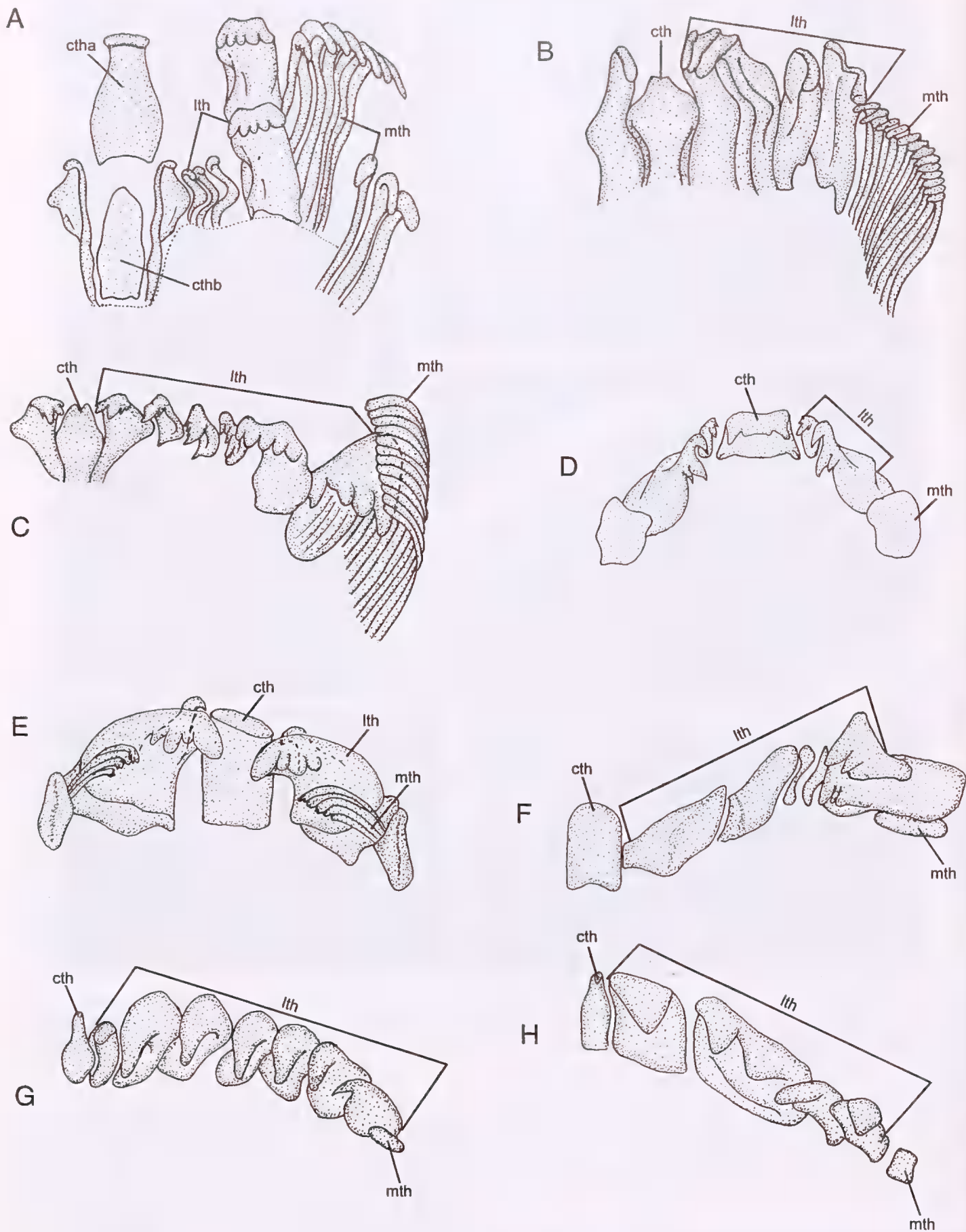


Figure 15.48 Superfamily Lepetelloidea, sections of radular tooth rows (not to scale). A, family Pseudococculinidae, with two examples of central teeth (cth, cthb); note overlapping functional row of marginal teeth and similarity of inner lateral teeth to those of Osteopeltidae and Pyropeltidae. B, family Pyropeltidae. C, family Osteopeltidae. D, family Lepetellidae. E, family Bathyphytophilidae, note the asymmetry of this radula type. F, family Addisoniidae. G, family Cocculinellidae. H, family Choristellidae. cth, central tooth; ctha, cthb, central tooth, two examples, a and b; lth, lateral teeth; mth, marginal teeth. (A, combined and modified after Hickman 1984c and Marshall 1986; B, after scanning electron micrographs of McLean & Haszprunar 1987 and McLean 1992b; C, after Marshall 1987; D, combined after Moskalev 1978 and Hickman 1983; E, after scanning electron micrographs of Haszprunar & McLean 1996; F, after scanning electron micrographs of Hickman 1983 and McLean 1985; G, after Marshall 1987; H, after scanning electron micrographs of McLean 1992a) [G. Haszprunar]

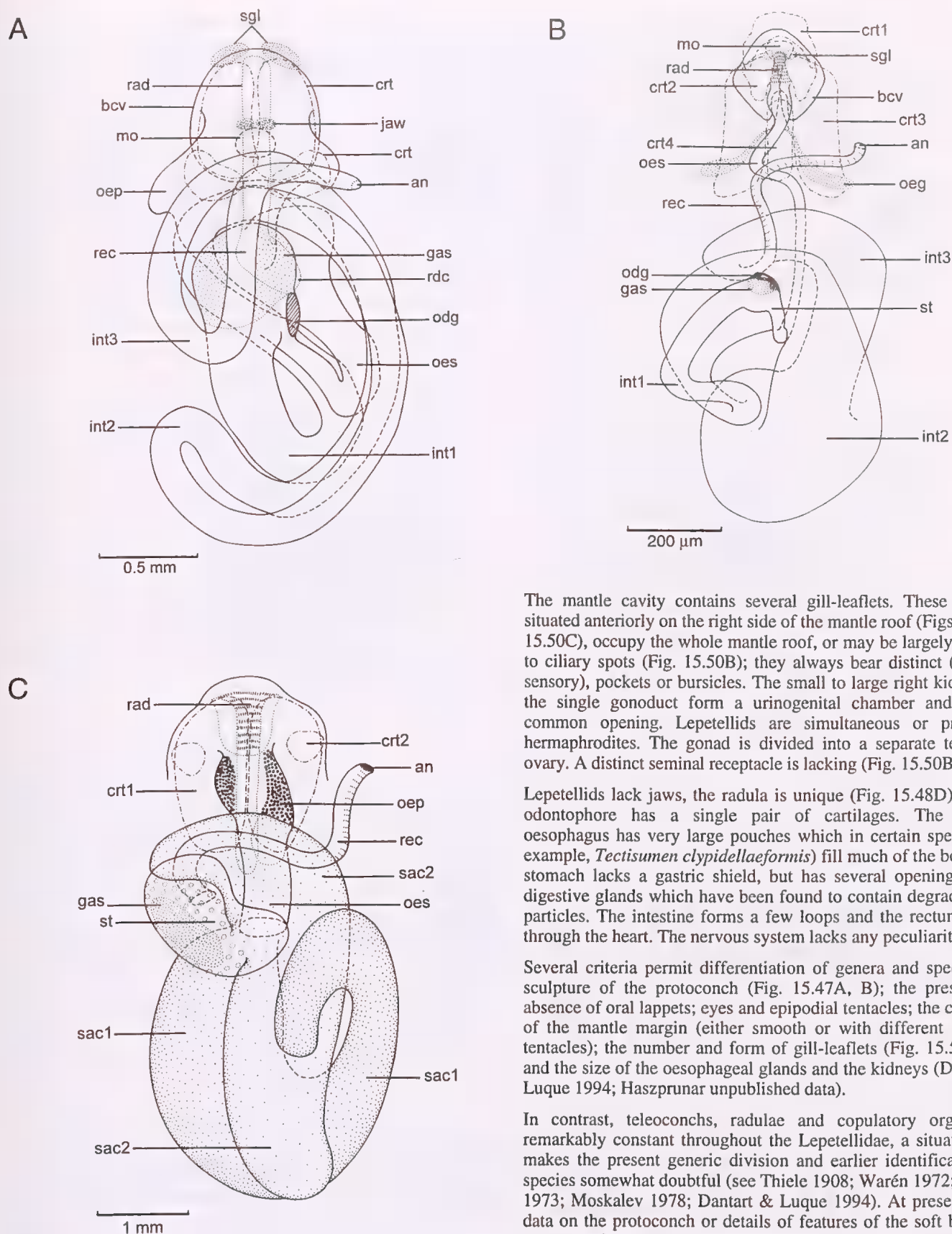


Figure 15.49 Superfamily Lepetelloidea. Reconstructed alimentary systems, dorsal view. A, family Pseudococculinidae, *Amphiplica knudseni*. B, family Cocculinellidae, *Cocculinella minutissima*. C, family Choristellidae, *Choristella hickmanae* (the 'circumoesophageal glands' are omitted). an, anus; bcv, buccal cavity; crt, cartilage; crt1, crt2, crt3, crt4, cartilage 1, 2, 3 or 4; gas, gastric shield; int1, int2, int3, intestinal loops 1, 2 or 3; jaw, jaw; mo, mouth opening; odg, opening of digestive gland; oeg, oesophageal gland; oep, oesophageal pouch; oes, oesophagus; rad, radula; rdc, radular caecum; rec, rectum; sac1, sac2 - cul de sac of possibly digestive gland 1 or 2; sgl, salivary glands; st, stomach. (A, after Haszprunar 1988d; B, after Haszprunar 1988e; C, after Haszprunar 1992a)

[G. Haszprunar]

The mantle cavity contains several gill-leaflets. These may be situated anteriorly on the right side of the mantle roof (Figs 15.46C, 15.50C), occupy the whole mantle roof, or may be largely reduced to ciliary spots (Fig. 15.50B); they always bear distinct (possibly sensory), pockets or bursicles. The small to large right kidney and the single gonoduct form a urinogenital chamber and have a common opening. Lepetellids are simultaneous or protandric hermaphrodites. The gonad is divided into a separate testis and ovary. A distinct seminal receptacle is lacking (Fig. 15.50B, C).

Lepetellids lack jaws, the radula is unique (Fig. 15.48D) and the odontophore has a single pair of cartilages. The anterior oesophagus has very large pouches which in certain species (for example, *Tectisumen clypidellaeformis*) fill much of the body. The stomach lacks a gastric shield, but has several openings to the digestive glands which have been found to contain degraded food particles. The intestine forms a few loops and the rectum passes through the heart. The nervous system lacks any peculiarities.

Several criteria permit differentiation of genera and species: the sculpture of the protoconch (Fig. 15.47A, B); the presence or absence of oral lappets; eyes and epipodial tentacles; the condition of the mantle margin (either smooth or with different types of tentacles); the number and form of gill-leaflets (Fig. 15.50B, C); and the size of the oesophageal glands and the kidneys (Dantart & Luque 1994; Haszprunar unpublished data).

In contrast, teleoconchs, radulae and copulatory organs are remarkably constant throughout the Lepetellidae, a situation that makes the present generic division and earlier identifications of species somewhat doubtful (see Thiele 1908; Warén 1972; Panetta 1973; Moskalev 1978; Dantart & Luque 1994). At present either data on the protoconch or details of features of the soft body are necessary for correct identification.

Family Pseudococculinidae

The Pseudococculinidae, with about 35 described species, are the largest cocculiniform family. Pseudococculinids are found worldwide, typically in deeper waters, ranging from 40 m to more than 5700 m. They live on various substrata, mostly on fresh, to largely decayed, wood, but some species are found on decaying algal holdfasts, and dead carapaces of deep-sea stone crabs (Lithodidae); *Amphiplica* (*Gordabyssia*) *gordensis* occurs in the hydrothermal-vent habitat (see Marshall 1986; Haszprunar 1988c, 1988d; McLean 1988c, 1991).

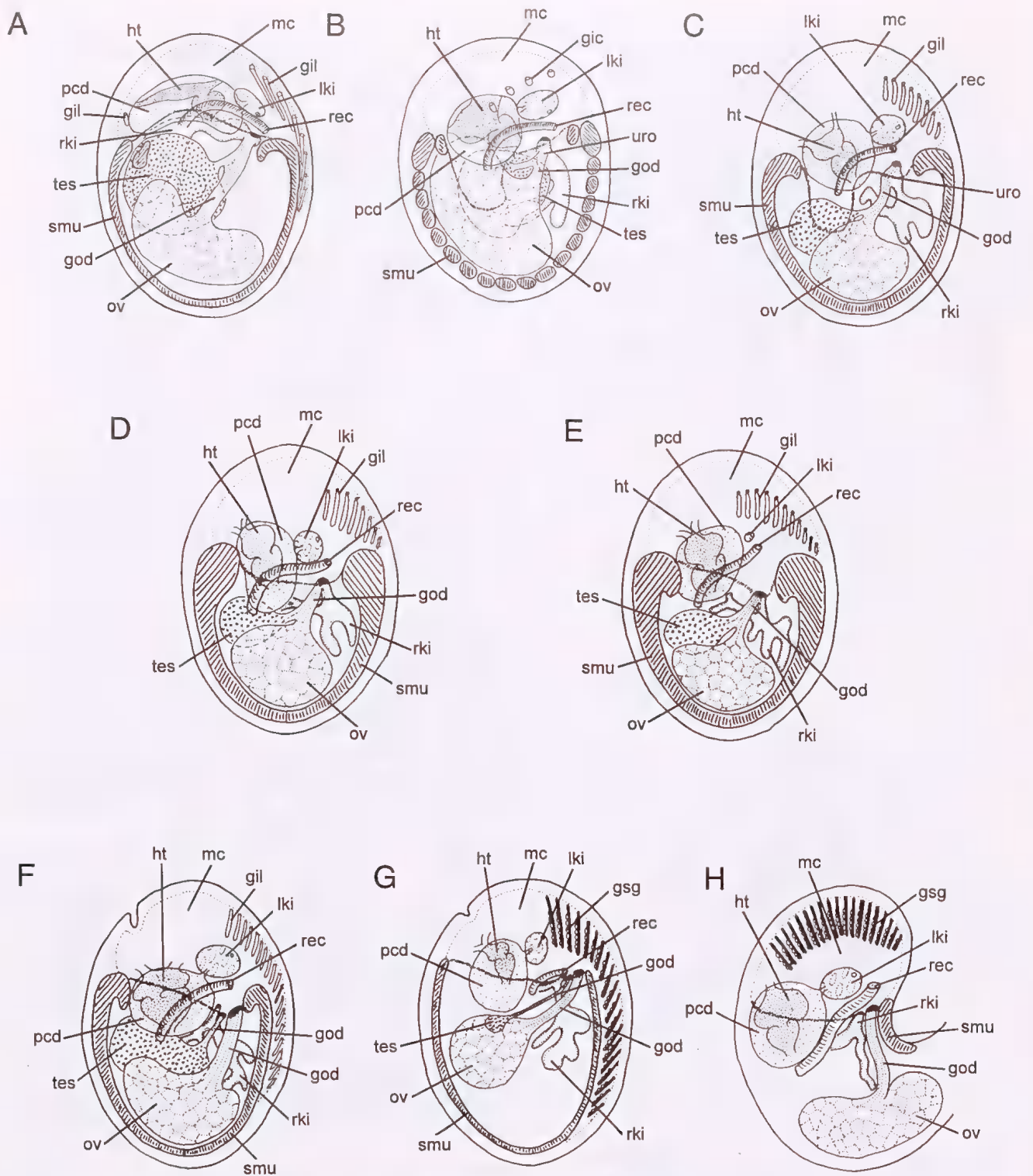


Figure 15.50 Superfamily Lepetelloidea. Semischematic diagrams of shell muscle, mantle cavity and gonopericardial system, dorsal view. A, family Bathyphytophilidae, *Bathyphytophilus diegensis*. B, C, family Lepetellidae: B, *Lepetella* sp.; C, *Lepetella tubicola*. D, family Pseudococculinidae, *Pseudococculina gregaria*. E, family Pyropeltidae, *Pyropelta musaica*. F, family Osteopeltidae, *Osteopelta mirabilis*. G, family Addisoniidae, *Addisonia lateralis*. H, family Chorisellidae, *Chorisella hickmanae*. gic, gill-leaflets reduced to ciliary spots; gil, gill-leaflets; god, gonoduct; gsg, gill leaflets with skeleton and glandular area; ht, heart; lki, left kidney; mc, mantle cavity; ov, ovary; pcd, pericardium; rec, rectum; rki, right kidney; smu, shell muscle; tes, testis; uro, urinogenital chamber. (A, modified after Haszprunar & McLean 1996; B, after Haszprunar unpublished; C–G, after Haszprunar 1988a) [G. Haszprunar]

The Pseudococculinidae include 13 nominal genera placed in the two subfamilies, Pseudococculinae and Caymanabyssiinae. Pseudococculinae are represented by *Pseudococculina*, *Notocrater*, *Tentaoculus*, *Kurilabyssia*, *Bandabyssia*, *Mesopelex*, and *Punctabyssia*, and the fossil genus *Kaiparapelta*. Caymanabyssiinae include the genera *Caymanabyssia* (incorporating the subgenus *Dictyabyssia*), *Colotrachelus*, *Yaquinabyssia*, *Copulabyssia* and *Amphiplica* (including subgenus *Gordabyssia*). These can be distinguished on characters of the protoconch and teleoconch, radula, external morphology and internal anatomy. The validity of the genus *Bandabyssia* and the subgenera *Dictyabyssia* and *Gordabyssia* requires verification

from anatomical characters (see Schepman 1908; Moskaliev 1976; Marshall 1986; Haszprunar 1988d; McLean 1988c, 1991). The extant Australian and New Zealand fauna includes 14 reported species in all of these genera except *Bandabyssia* and *Yaquinabyssia* (see Schepman 1908; Suter 1908; Thiele 1909; Finlay 1927a; Moskaliev 1976; Marshall 1986; Haszprunar 1988c, 1988d; McLean 1988c, 1991).

Pseudococculinids characteristically have an oval aperture and a subcentral to posterior apex. The radula is a diagnostic rhipidoglossate type (Hickman 1983; Marshall 1986).

Pseudococculinid shells are thin and porcellaneous, range in length from 1.5–15 mm and have concentric and/or granulate sculpture (Fig. 15.45E, F, I, K). A septum is present in the New Zealand species *Tentaoculus haptricola* (Fig. 15.45J). The protoconch is often eroded in adults, has a fused tip, and shows various sculptural patterns, such as reticulate ribs, anastomosing threads, or fine prismatic crystals, which are diagnostic for genera (Figs 15.45G, H, 15.47C, D). A pedal gland may be retained in adults of some species and a single pair of epipodial tentacles is present in all species. Among Pseudococculininae, eyes occur in all stages of reduction, whereas species of the subfamily Caymanabyssiinae lack eyes. The features of the right cephalic tentacle, which is the copulatory organ, are diagnostic for genera (Fig. 15.46F–H; Marshall 1986; Haszprunar 1988d). In *Pseudococculina* and *Notocrater* species, the seminal groove is more highly derived, forming a tube, and their copulatory organs are also tubular.

Several gill-leaflets, bearing distinct (sensory?) bursicles, are situated antero-dorsally on the right, or on both sides, of the shallow mantle cavity. The right kidney and the single gonoduct form a common urinogenital opening, and a distinct receptacle is not present (Fig. 15.50D).

Oral lappets are generally present (Fig. 15.46E) and the paired jaw consists of tooth-like elements. The form of the rhipidoglossate radula (Fig. 15.48A) is diagnostic for family, genera and species. Two pairs of radular cartilages and a radular caecum are present. The alimentary tract, genital and nervous system do not show distinct specialisations. The anterior oesophagus has glandular pouches, and the large stomach contains a gastric shield, but lacks a protostyle and a diverticulum. The digestive gland has single lobe. There are several intestinal loops and the rectum passes through the heart (Fig. 15.49A).

Family Osteopeltidae

The Osteopeltidae are a very small family of symmetrical limpets. Although only three species, *Osteopelta mirabilis* (from the Chatham Rise and off Chatham Islands; 880 m), *O. ceticola* (from off Iceland, 880–955 m) and *O. praeceps* (from off New Zealand, 370–912 m), have been described (Marshall 1987, 1994; Warén 1991), the family probably has (or at least had) a worldwide distribution. All osteopeltid species live and feed on whale bones, a habitat similar to the hydrothermal-vent habitat in its characteristics, such as a high level of hydrogen sulphide (Smith, Kukert, Weatcroft, Jumars & Deming 1989).

Osteopeltids have an oval shell aperture and a distinct type of rhipidoglossate radula. The long gill leaflets lack bursicles. There are separate openings for the right kidney, oviduct and vas deferens; a seminal receptacle is lacking. Small radular cartilages and distinct oesophageal glands characterise the alimentary tract. The cerebropedal nervous system is concentrated, and the eyes are reduced.

The osteopeltid shell is white, thin, and ranges up to about 8 mm in length. Its apex is subcentrally situated, and the (unknown) protoconch is eroded in adults. The snout is tapered (Fig. 15.46B), and a single pair of epipodial tentacles is present; oral lappets and a pedal gland are lacking. The pigmented eyes are sunken and situated adjacent to the cerebral ganglia. The mantle forms an inhalant siphon at the anterior left side (Fig. 15.46B). The right cephalic tentacle is only slightly modified by a seminal groove to form the copulatory organ (Marshall 1987; Warén 1989).

Many prominent gill-leaflets are present in the right subpallial cavity and antero-dorsally in the shallow mantle cavity (Fig. 15.50F). Bursicles, as found in some other lepetelloidean families, are absent. The right kidney has a separate opening, and the testis and ovary have their own ducts and openings. Condensed sperm have been found near the ovary in *Osteopelta mirabilis* (Haszprunar 1988e).

The paired jaws consist of tooth-like elements. The rhipidoglossate radula is diagnostic for the family (Fig. 15.48C) and one pair of small cartilages and a radular caecum are present. The anterior oesophagus has large oesophageal glands, and the stomach contains a gastric shield, but lacks a protostyle and a diverticulum. A paired digestive gland is present. There are few intestinal loops, and the rectum passes through the heart.

In contrast to that of other lepetelloidean families, the hypoathroid cerebropedal nervous system of osteopeltids is more concentrated, forming a closed ring posterior to the radular cartilages. Advanced features are also found in the pedal nerve system which has true ganglia instead of pedal cords. In contrast, the streptoneurous visceral loop is primitive, being very wide and weakly ganglionate (Haszprunar 1988e, 1988c). An osphradial epithelium is lacking; the very small statocysts contain several statoconia.

Family Cocculinellidae

Cocculinellidae are a family of symmetrical limpets, found in shallow (13 m) to moderately deep (250–450 m) waters. The single genus *Cocculinella* includes one Australian (*C. coerita*) and two New Zealand species (*C. kopua*, *C. osteophila*) (Smith 1904; Thiele 1909; Moskalev 1971, 1978; Marshall 1983a, 1986), and the type species (*C. minutissima*) from off the Andaman Islands (Indian Ocean). All cocculinellid species live and feed on fish bones.

Cocculinellids have a narrowly elliptical aperture and subcentral apex. The radula is largely modified and highly diagnostic. The kidneys, testis and ovary have separate openings. The alimentary tract is characterised by a lack of jaws, and by having small, true oesophageal glands, a vestigial stomach, and a largely expanded part of the intestine. The cerebral ganglia are very close to each other.

The thin shell is 2–3 mm in length and exhibits a weak, concentric sculpture (Fig. 15.45L, M). The apex is subcentral. The protoconch, which is often retained in adults, has a fused tip and has no significant sculpture (Fig. 15.47E). Oral lappets, pedal gland, epipodial tentacles and eyes are lacking and the mantle edge is simple (Fig. 15.46D). The right cephalic tentacle is slightly modified as a copulatory organ, having a seminal groove (Smith 1904; Thiele 1909; Marshall 1983a; Haszprunar 1988e).

The anterior right section of the roof of the shallow mantle cavity may bear several gill-leaflets (*C. osteophila*) or two ciliary spots (*C. minutissima*). The opening of the right kidney is separate from that of the gonoducts. The testis and ovary have separate ducts and openings. A seminal receptacle is not present.

Cocculinellids lack jaws, and the unique radula (Fig. 15.48G) is supported by two pairs of radular cartilages and a radular caecum. The anterior oesophagus has a number of small oesophageal glands. The stomach is reduced, but a gastric shield and a prominent digestive gland are present. The proximal intestine forms a large sac-like organ and the rectum passes through the heart (Fig. 15.49B).

Because of its small size, the hypoathroid cerebropedal ring of the nervous system appears quite concentrated; the cerebral ganglia in particular are connected by a very short commissure. In contrast, the streptoneurous visceral loop is primitively very wide and shows only very small ganglia (Haszprunar 1988c, 1988e).

Family Choristellidae

Members of the Choristellidae (= Choristidae of various authors) are the only Cocculiniformia to have coiled shells. Radular and anatomical characters confirm the close affinity of choristellids with Cocculinellidae and Addisoniidae (Moskalev 1978; Hickman 1983; Haszprunar 1988c, 1992a; McLean 1992a). Two genera (*Choristella* and *Bichoristes*) and eight species have been described (McLean 1992a). Species occur worldwide in bathyal to abyssal depths. Like addisoniids, all choristellid species live and feed on empty egg-cases of sharks or skates.

15. PROSOBRANCHS

Until recently *Choristella* was the only valid genus in Choristellidae (see Bouchet & Warén 1979; McLean 1992a). However, McLean (1992a) in a recent revision recognised an additional genus, *Bichoristes*. The Australian and New Zealand fauna includes two species, *Choristella ponderi* (from off Queensland and New South Wales) and *C. marshalli* (from off New Zealand).

The coiled shell is small (2–10 mm diameter), thin, of three to three and a half rounded or keeled whorls in *Choristella* or *Bichoristes*, respectively. The suture is deeply channelled. The tip of the large protoconch (250–300 µm) is bulbous, and its surface smooth. The radula is strongly modified and diagnostic. Many prominent gill-leaflets hang from the mantle roof. The gill-leaflets include skeletal rods and a distinct glandular area, but lack bursicles. The genital opening in each sex is discrete. The alimentary tract is characterised by paired, prominent jaws, a unique gland around the posterior oesophagus, and a very short intestine.

The shell is extremely thin with a rounded or keeled aperture (Fig. 15.45N), and a narrow to wide coiled umbilicus. Though the protoconch is rarely retained in adults, the operculum of three to ten whorls is retained (Fig. 15.45N). The oral lappets are prominent, and a pedal gland and several pairs of epipodial tentacles are present. Additional blunt tentacles occur on both sides behind the cephalic tentacles. The right cephalic tentacle is modified for its copulatory function by a seminal groove that continues backwards along the right side of the neck.

The left kidney is situated in the mantle roof and is connected with the pericardium. The branches of the right kidney spread between the viscera and open separately from the gonoduct. Choristellids are gonochoristic, and in both sexes the simple gonoduct has its own opening (Fig. 15.50H). In females, a distinct seminal receptacle for sperm storage is present on the left side.

The jaws are prominent and the salivary glands form pouches. The choristellid radula (Fig. 15.48H; McLean 1992a) resembles that of the Cocculinellidae, and is supported by two pairs of modified cartilages. The anterior oesophagus is narrow, but has lateral pouches, and the posterior oesophagus is embedded in a 'circumoesophageal gland' of uncertain homology (omitted in Fig. 15.49C). The stomach is prominent and has a gastric shield, but lacks a style sac. The digestive glands are highly modified, forming huge cul-de-sacs which contain food particles. The intestine is very short, the rectum passes beneath the heart (Fig. 15.49C). The nervous system shows no distinctive features. Eyes are lacking, but an osphradial epithelium is present.

Superorder VETIGASTROPODA

The Vetigastropoda (*sensu* Salvini-Plawen 1980; Salvini-Plawen & Haszprunar 1987) comprises the superfamilies Fissurelloidea, Pleurotomarioidea, Trochoidea and Seguenzioidae. It includes the most plesiomorphic living orthogastropods, some still retaining both sets of the pallial and renopericardial organs. The group first appears in the Upper Cambrian (Knight, Cox, Keen, Batten, Yochelson & Robertson 1960b), and many subclades have become extinct during its long history.

Haszprunar (1988a) included the Pleurotomarioidea, Haliotoidea and Scissurelloidea, Lepetodriloidae (one of the deep-sea hot-vent taxa, McLean 1988a; Fretter 1988) and Trochoidea in the Vetigastropoda, but placed the seguenziids in a different group, although he later (Haszprunar 1993) placed them in Vetigastropoda. Ponder & Lindberg's (1996, 1997) analyses indicate that the probably paedomorphic Lepetelloidea (see Cocculiniformia) and Seguenzioidae are part of this clade. Some of the extinct, bilaterally symmetrical Bellerophonitoidea probably also belong here.

Often regarded as 'primitive', the Vetigastropoda is one of the most successful and distinctive gastropod clades (Hickman 1988), being well supported by several apomorphies including epipodial

sense organs, tentacles with sensory papillae, bursicles and papillate digestive gland, although heterochronic loss of one or more of these characters has occurred in some taxa. A slit or holes are often developed in the shell of the more primitive taxa. The loss of this slit is usually associated with the loss of the post-torsional right pallial organs, an event that has occurred independently in several lineages. A special cell type in the osphradium ('cilia bottles', Haszprunar 1985a) also appears to be a synapomorphy among higher vetigastropods, though details are not known for all groups. A spiral gastric caecum is characteristic of some vetigastropods and is not found in other gastropods. Plesiomorphic features shared by Vetigastropoda and Neritopsina include the rhipidoglossate radula.

The rhipidoglossate radula has some distinctive features (Hickman 1984c), the central part of each row being occupied by rows of teeth modified into plates. The small central teeth (for this section the term 'rachidian' is used) are flanked sequentially each side by a broad lateral tooth, relatively small second and third lateral teeth and a massive fourth lateral tooth.

The Cocculinoidea and the Lepetelloidea were included in the Cocculiniformia by Salvini-Plawen & Haszprunar (1987) and Haszprunar (1988c), and are treated as a unit herein, although Haszprunar (1993) admitted the possibility that the group is not monophyletic. Ponder & Lindberg's (1996, 1997) analyses suggest that cocculinoideans and lepetelloideans belong in very different clades. Cocculinoideans are of uncertain affinities, possibly related to neritopsines, whereas lepetelloideans may be derived, simplified members of the vetigastropod clade.

Superfamily PLEUROTOMARIOIDEA

The Pleurotomarioidea includes the most primitive of the living vetigastropods recognised here. Members of the superfamily are most readily recognised by a conspirally coiled adult shell with a distinctive slit or emargination in the outer lip that leaves a distinctive trace as a selenizone or series of tremata (Figs 15.51A–C, 15.52A–D, 15.53A–D). Nacreous aragonitic microstructure predominates in the shells of most forms, to the near exclusion of aragonitic crossed structures. Calcitic microstructures are rarely present.

All three of the extant pleurotomarioidean families are represented in the extant Australian fauna, Pleurotomariidae by a single species in deep water off the North West Shelf; Scissurellidae by a dozen named species from relatively shallow water, poorly studied and known primarily from empty shells; and Haliotidae by a diverse assemblage of genus-group taxa represented by a number of species that are abundant, economically significant, and well studied. There is no comprehensive modern review of the superfamily in Australia, but Cotton (1959a) listed most of the available names for the Australian species.

The three families exhibit extremes in vetigastropod shell morphology. Living pleurotomariids are among the largest conspirally coiled vetigastropods, with shells up to 200 mm high and contain a predominance of nacreous aragonite. Scissurellids are among the smallest, with minute conspiral shells that lack nacreous aragonitic structure and are usually less than 3 mm high. Rapid expansion of the final whorl produces limpet-like forms in some deep-water taxa, but the operculum is always retained. The same phenomenon occurs in a few scissurellid taxa, but in these the operculum is retained. Haliotids, on the other hand, always lack an operculum. The haliotid shell has been modified by flattening of the middle and inner nacreous layers, and dramatic expansion of the final whorl to produce a limpet-like form with a series of characteristic tremata.

The epipodium is unspecialised relative to that of trochoideans, and lacks cephalic lappets and neck lobes. However, there may be numerous epipodial sensory papillae and tentacles, especially in haliotids.

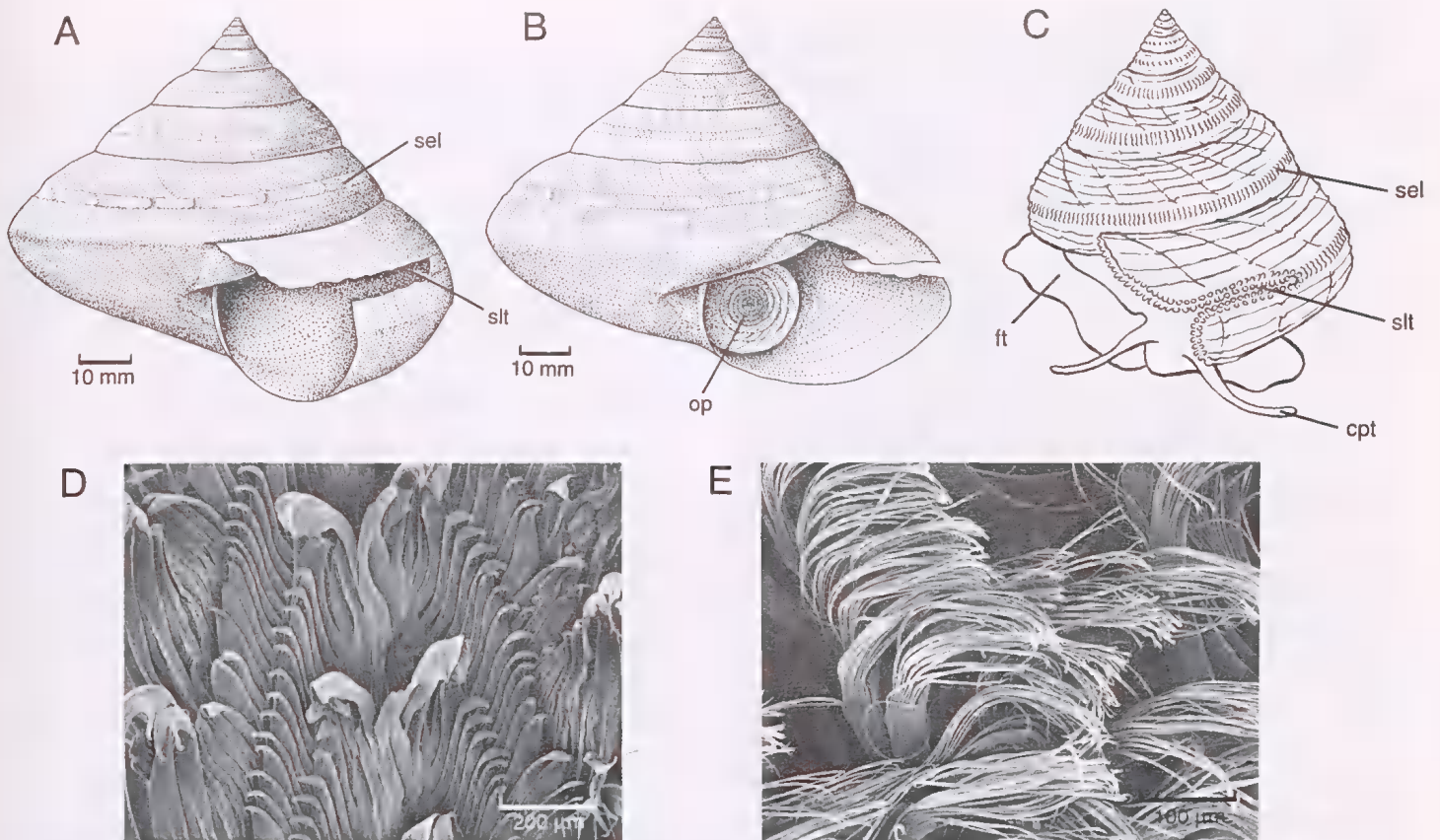


Figure 15.51 Family Pleurotomariidae. A, B, *Pleurotomaria westralis*: A, adult shell, showing the distinctive slit in the outer lip and selenizone; B, shell with the operculum deeply retracted. C, diagrammatic representation of the relationship of the shell and the living animal. D, E, portions of radulae of two Western Atlantic species: D, *Pleurotomaria quoyana*, central section; E, *Pleurotomaria midas*, marginal bristle teeth. cpt, cephalic tentacle; ft, foot; op, operculum; sel, selenizone; slit, slit.

All members of the superfamily retain the primitive vetigastropod condition of bilateral symmetry of the mantle cavity, with paired ctenidia, osphradia and hypobranchial glands. The ctenidia have well-developed skeletal rods and long efferent membranes. As in Fissurelloidea and Trochoidea, the heart has two functional auricles. There are two kidneys, but they are asymmetric in size and form: the left is smaller, with numerous papillae projecting into the lumen (the so-called 'papillary sac'). A single right gonad is present, and gametes pass first through a duct of gonadal tissue to a renopericardial duct that joins the anterior end of the right kidney, and finally into the mantle cavity through glandular mantle tissue (an open pallial gonoduct). Sexes are separate. Gametes are usually shed directly into the water column and fertilisation is usually pelagic. Larval development, too, is usually pelagic, and the larvae are non-feeding (lecithotrophic). The nervous system is streptoneurous and hypoathroid.

The radula is rhipidoglossate and sufficiently distinct in each of the families that it is not possible to postulate a primitive condition for the radula. A broad range of diets is represented, ranging from feeding selectively on sponges and other sessile invertebrates to cropping macroalgae or grazing on surface films.

The three pleurotomarioidean families show different patterns of specialisation with respect to habitat, substratum, and biogeographic distribution. Living pleurotomariids are restricted to rock walls, tops of seamounts, or patches of firm substratum in deep, cold water (below 200 m). Scissurellids occur primarily at high, temperate latitudes in shallow water on marine algae, but there are some deep-water taxa, including some highly derived forms at hydrothermal vents. Haliotids occur over a broad latitudinal range, primarily in shallow water and on firm substrata that permit clamping of the shell by the foot.

The fossil record of the superfamily extends back to the Middle Cambrian period, and a number of extinct Palaeozoic and Mesozoic families of conispirally coiled pleurotomarioideans are

known from Australia. The extinct families, reviewed by Knight *et al.* (1960b), are based on shell characters that may prove homoplasious. For example, the position of the shell slit in some of the extinct families suggests an underlying anatomical organisation that is not pleurotomarioidean (Hickman unpublished data). The first records of scissurellids and haliotids are from Mesozoic rocks, but the evolutionary radiation of both families is confined to the Cainozoic Era. Both are present in the Australian fossil record, scissurellids appearing in the Eocene and haliotids in the Miocene (Hickman unpublished data). Haszprunar (1989) restricted Pleurotomarioidea to the single family Pleurotomariidae, but the argument to exclude the 20 extinct pleurotomarioidean families and to place Scissurellidae and Haliotidae in their own separate orders is speculative with respect to the anatomical organisation of extinct taxa and uninformative with respect to their systematic placement.

Family Pleurotomariidae

Of the 21 families of conispirally coiled pleurotomarioideans (Knight *et al.* 1960b), only the family Pleurotomariidae has living representatives. Living pleurotomariids have large shells relative most extinct pleurotomarioideans. The slit is clearly expressed on earlier whorls as a selenizone or slit-band; it reflects the underlying primitive anatomical condition of paired bipectinate ctenidia that lie on each side of the slit in a deep, narrow mantle cavity. The family is diagnosed tentatively (in the absence of anatomical data from the extinct taxa) by a series of highly specialised features of the radula.

Living pleurotomariids were unknown from the Australasian region until 1982 when Bouchet & Metivier reported two new species from New Caledonia and the Lau Ridge between Fiji and New Zealand. The following year, Slack-Smith (1983) reported the first Australian specimen, trawled alive from the North West Shelf off Port Hedland. Many specimens have been collected

15. PROSOBRANCHS

subsequently from the area, confirming that it is common in the bathyal fauna. New records of pleurotomariids from seamounts off eastern Australia accumulate as this region is explored more thoroughly.

The living species are united under a single genus, *Pleurotomaria*, or alternatively allocated among the genera *Perotrochus*, *Entemnotrochus* and *Mikadotrochus*. The anatomy of living pleurotomariids was documented by Fretter (1964, 1966). Summaries of the living species are provided by Bayer (1965) and Bouchet & Metivier (1982), and the biogeography, ecology, and Cainozoic fossil record were summarised by Hickman (1976, 1984a). The structure and function of the pleurotomariid radula are discussed by Hickman (1984b). The most comprehensive illustrations of living pleurotomariid shells are the 46 colour photographs published by Matsukuma, Okutani & Habe (1991).

The pleurotomariid shell (Fig. 15.51A, B) is trochoidean in outline, with a distinct peripheral demarcation that ranges from rounded to sub-angular. The apical profile varies from convex to concave, and the base of the shell ranges from flat to convex, with an umbilicus that may be open or closed by a callus deposit and thickening of the columella. The ornamentation on the shell is predominantly spiral. Shell pigmentation is variable, but most commonly the ground colour is a pale creamy salmon with discordant axial streaking in a darker rust colour. The interior nacre is thick and conspicuous and extends to the growing margin of the shell. The operculum is small relative to the size of the final aperture, and is very deeply retracted when the animal withdraws into the shell (Fig. 15.51B).

Features of the external morphology of the animal and its relationship to the shell are illustrated in Figure 15.51C. The foot is broadly rounded anteriorly, with the pedal gland located in a distinct slit separating the propodium and mesopodium. The foot tapers posteriorly and has a deep median longitudinal groove on the posterior dorsal surface. The snout is short and bluntly rounded anteriorly. The cephalic tentacles are thick and fleshy, and the eyes are on low protuberances rather than eye stalks. The epipodium is poorly developed, lacking epipodial tentacles, enlarged sensory papillae, necklobes, and cephalic lappets. The edge of the mantle is finely papillate and can be enrolled into a pseudosiphon within the slit to direct the exhalant flow of water from the mantle cavity.

The hystricoglossate radula (Fig. 15.51D, E), a specialised form of rhipidoglossate radula, was discussed and figured by Hickman (1984a, 1984b). The radula has an asymmetric central tooth field (Fig. 15.51D) containing a rachidian and numerous lateral teeth of two distinct types. There are also two distinct types of marginal teeth. The inner sickle teeth are the most formidable teeth in the radula, and are flanked by the bizarre filament-tipped teeth (Fig. 15.51E) that are the hallmark of the pleurotomariid radula. It is now firmly established that sponges comprise a major portion of the diet.

Living pleurotomariids occur on firm substrata, predominantly at bathyal depths (below 200 m). Although they were once considered extremely rare and commanded high prices as collectors' items, a number of species are now known, from submersible observations, to be abundant in their natural habitats. Species occurring on rock outcrops and under rock ledges are difficult to collect by normal sampling methods.

The family originated in the Triassic. Its diversity declined dramatically during the Mesozoic and Cainozoic eras, with extinction of shallow-water taxa occurring by the close of the Neogene (Hickman 1976). Three Late Cretaceous (Maastrichtian) pleurotomariids have been described in the extinct genera *Conotomaria* and *Leptomaria* (Darragh & Kendrick 1994). Although there are only two named Neogene species of *Pleurotomaria*, *P. bassi* and *P. tertiaria*, there are at least five undescribed Eocene species (C.S. Hickman personal observation).

Family Scissurellidae

Members of this highly derived family retain the paired ctenidia and paired hypobranchial glands. The shell has a slit, is small and relatively thin, and lacks conspicuous interior nacre. Two shell muscles are retained or fused into a single horseshoe-shaped columellar muscle. The operculum is always retained. Scissurellid systematics were reviewed by Herbert (1986), and expanded substantially by McLean (1989b) and Haszprunar (1989), following study of new forms from deep-sea hydrothermal vents. Australian scissurellids were reviewed by Cotton (1959a). Some authors (for example, Haszprunar 1989; McLean 1989b) have removed the Scissurellidae from the Pleurotomarioidea and elevated it to ordinal rank, but these authors also favour removing haliotids and restricting the Pleurotomarioidea to a single extant family.

The family Scissurellidae contains nine genus-level taxa, three of which are known only from deep-sea hydrothermal vents. Four of the remaining six taxa (*Scissurella*, *Anatoma*, *Scissurona* and *Sinezona*) are represented in the Australian fauna. *Scissurella*, *Anatoma* and *Sinezona* are cosmopolitan, whereas *Scissurona* is currently known only from Australia and New Zealand, and appears to be closely related to the endemic New Zealand genus *Incisura*. The family is well represented in Australia and New Zealand, with 26 named species; worldwide there are approximately 60 species. Material in museum collections indicates that there are many more undescribed Australian species, and a review of the family is overdue.

The minute to small shells (<3 mm) (Fig. 15.52A–D) are frequently translucent, unpigmented, and characteristically covered with extremely fine cancellate or axial sculpture. The scissurellid protoconch, illustrated by Herbert (1986), ranges from smooth (for example, *Sukashitrochus*) to sculptured with strong axial ribs (for example, *Scissurella* and *Sinezona*), and the terminal lip of the protoconch is frequently thickened. The position of the slit varies from the periphery to high on the shoulder. The slit is narrow and deep in contrast to the labral sinuses in the superficially similar shells of seguenziid gastropods. The narrow umbilicus may be either open or closed, and the inner lip may be reflected and thickened into an umbilical cord. Several distinctive shell modifications are seen within the family. The terminal closure of the slit in some taxa leaves an elongate to circular foramen in the shell (Fig. 15.52D). The expansion of the aperture and adoption of secondary bilateral symmetry and limpet form has occurred independently in the hydrothermal vent subfamily Temnocinclinae and in the closely related scissurelline genera, *Incisura* and *Scissurona*. Both modifications are seen in the Australian and New Zealand faunas.

The foot is ovate to elongate in outline and the anterior end has a pedal gland within a distinct slit between the propodium and mesopodium. The foot is folded longitudinally rather than transversely during retraction, and the operculum may be displaced to the left side of the foot, as in the genus *Sukashitrochus* (Haszprunar 1988f). Some scissurellids can expand the metapodium to form a 'fin' and are able to 'swim' for short distances through the water column (Haszprunar 1988f).

The epipodium is more differentiated than in pleurotomariids, with as many as seven pairs of epipodial tentacles. It is less differentiated than in trochoideans, however, lacking cephalic lappets and neck lobes. The cephalic tentacles are slender and conspicuously micropapillate in some forms, although micropapillae are always lacking on the epipodial tentacles. The mantle edge is finely papillate and may be elaborated into mantle tentacles that emerge from the slit. The paired ctenidia are primitively bipectinate and the left is larger than the right, but in derived forms the ctenidia may be monopectinate and of equal size.

The most complete description of scissurellid anatomy is that of Bourne (1910). The works of Herbert (1986) and Haszprunar (1988f) provide references to accounts containing additional anatomical information. The numbers and basic features of other pallial organs (osphradia, hypobranchial glands), heart, kidneys,

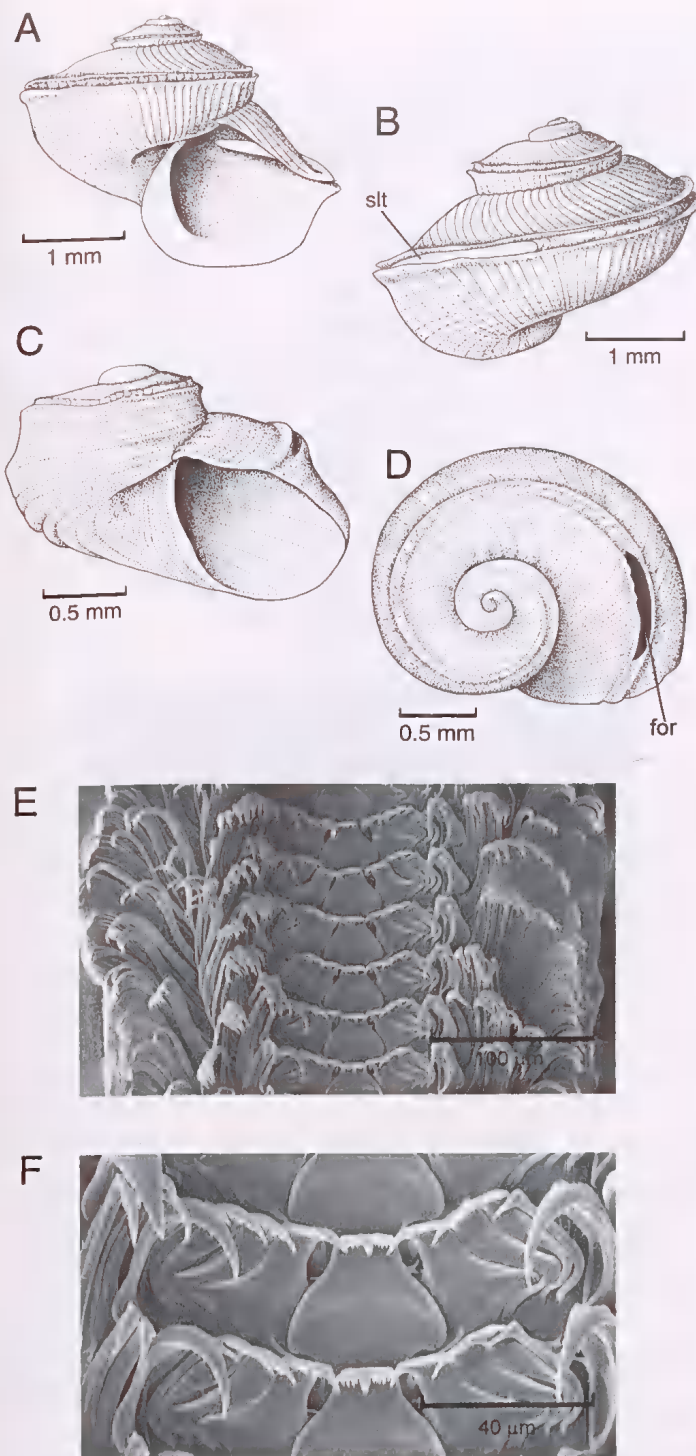


Figure 15.52 Family Scissurellidae. A, B, *Anatomia australis*, shell with an open slit on the peripheral demarcation: A, apertural view; B, abapertural view. C, D, *Sinezona* sp., shell with an ovate, closed slit (foramen) on the shoulder: C, apertural view; D, apical view. E, F, *Scissurella crispata*, from the North Atlantic, portions of radula: E, mid-section showing all teeth across a few transverse rows; F, details of central tooth-field. for, foramen; slit, slit.

[A–D, S. Weidland; E, F, C.S. Hickman]

gonads and nervous system are as described for the superfamily. Healy (1990c) has examined the sperm ultrastructure of an Australian scissurellid and determined that it is highly modified relative to other vetigastropods in having a deep basal invagination of the nucleus housing the centriolar complex and proximal portion of the axoneme, a laterally compressed nucleus, a midpiece consisting of a single, large mitochondrion partly sheathing the axoneme, frequent overlap of the mitochondrion with the base of the nucleus, and the presence of a perinuclear sheath. These features can be derived from the vetigastropod ect-aquasperm type, and it is as yet unknown whether they are characteristic of all scissurellids.

The radula (Fig. 15.52E, F) is symmetrical and of a derived rhipidoglossate grade, with reduction of the number of lateral teeth to five, as in trochoideans, or fewer. The distinctive rachidian has a broad, expanded base and a finely denticulate cusp with an enlarged median denticle. The lateral teeth have expanded outer limbs that interlock into pockets on adjacent teeth. The fourth lateral typically has a greatly reduced shaft and cusp, and the fifth lateral is greatly enlarged. Feeding habits and diets are poorly understood.

In shallow water, scissurellids are typically associated with marine plants and are commonly collected live by washing algal blades and holdfasts. Live animals also may be recovered from intertidal shell gravel in crevices, protected pools, and under rocks, suggesting a semi-interstitial mode of life for some species. Subtidally, animals are most commonly recovered from coarse clastic substrata. The family ranges from intertidal to abyssal, and although it is best known in Australia from cooler water and higher latitudes, there are many, as yet unnamed, tropical species.

Scissurellids are neither diverse nor abundant in the Australian fossil record, but an undescribed species is present from the Eocene (Hickman unpublished data) onward. The family first appears in Triassic rocks in Europe (K. Bandel personal communication) and had apparently spread to North America by the end of the Mesozoic Era (Knight *et al.* 1960b).

Family Haliotidae

The Haliotidae are diagnosed by a very high rate of apertural expansion and low rate of apertural translation during growth of the conispirally coiled shell, producing a low-spired 'limpet' with a large, muscular, clamping foot. The right shell muscle is greatly enlarged and the mantle cavity is displaced to the left. The left shell muscle is retained, but is very small. The operculum is lost, but the animal retains the primitive conditions of the pallial organs: paired bipectinate ctenidia, osphradia and hypobranchial glands. A hallmark of the haliotid shell is the series of respiratory holes (tremata, Fig. 15.53A; Pls 22.4, 22.5) that are formed during growth near the periphery of the shell and which are analogous to the pleurotomariid and scissurellid slit. The youngest five to eight holes are open, and although it is commonly stated that they serve an exhalant function, the anteriormost holes have been confirmed to be inhalant (Voltzow 1983). Haliotids are commonly known as abalone, sea ears, ear shells or muttonfish in Australia, paua in New Zealand, ormers in Great Britain, and venus ears or perlemoen in southern Africa.

Members of the family are usually classified under a single genus, *Haliotis*, which has been subdivided into eleven to sixteen subgenera (Cox in Knight *et al.* 1960b; Lindberg 1992). Six of the subgenera (*Exohaliotis*, *Marinauris*, *Notohaliotis*, *Ovinotis*, *Sanhaliotis* and *Schizmotis*) are endemic to Australasia, and there is precedence (for example, Cotton 1959a; Iredale & McMichael 1962) for elevating them to generic status. More than sixty specific epithets have been applied to Australian abalones, although the number of living and fossil species represented in the Australian fauna is closer to twenty-five. Australasia is a region of unusually high haliotid diversity.

Although there is no recent revision of the Australian species, a large body of literature treats the basic biology, ecology, and life histories of the commercially important species (for example, Shepherd 1973; Wells & Keasing 1989 and references therein). Lindberg (1992) mapped the geographic distribution of ten temperate Australian species in the context of a general overview of haliotid evolution and systematics.

The shells (Fig. 15.53A–D) are ornamented by a combination of spiral and axial ribs that frequently are nodose. Pigmentation is variable and may reflect diet, especially in species that feed on red algae (Ino 1952). The interior nacre is especially well developed. The middle and inner aragonitic layers are predominantly columnar nacre, whereas the thin outer layer may contain both

15. PROSOBRANCHS

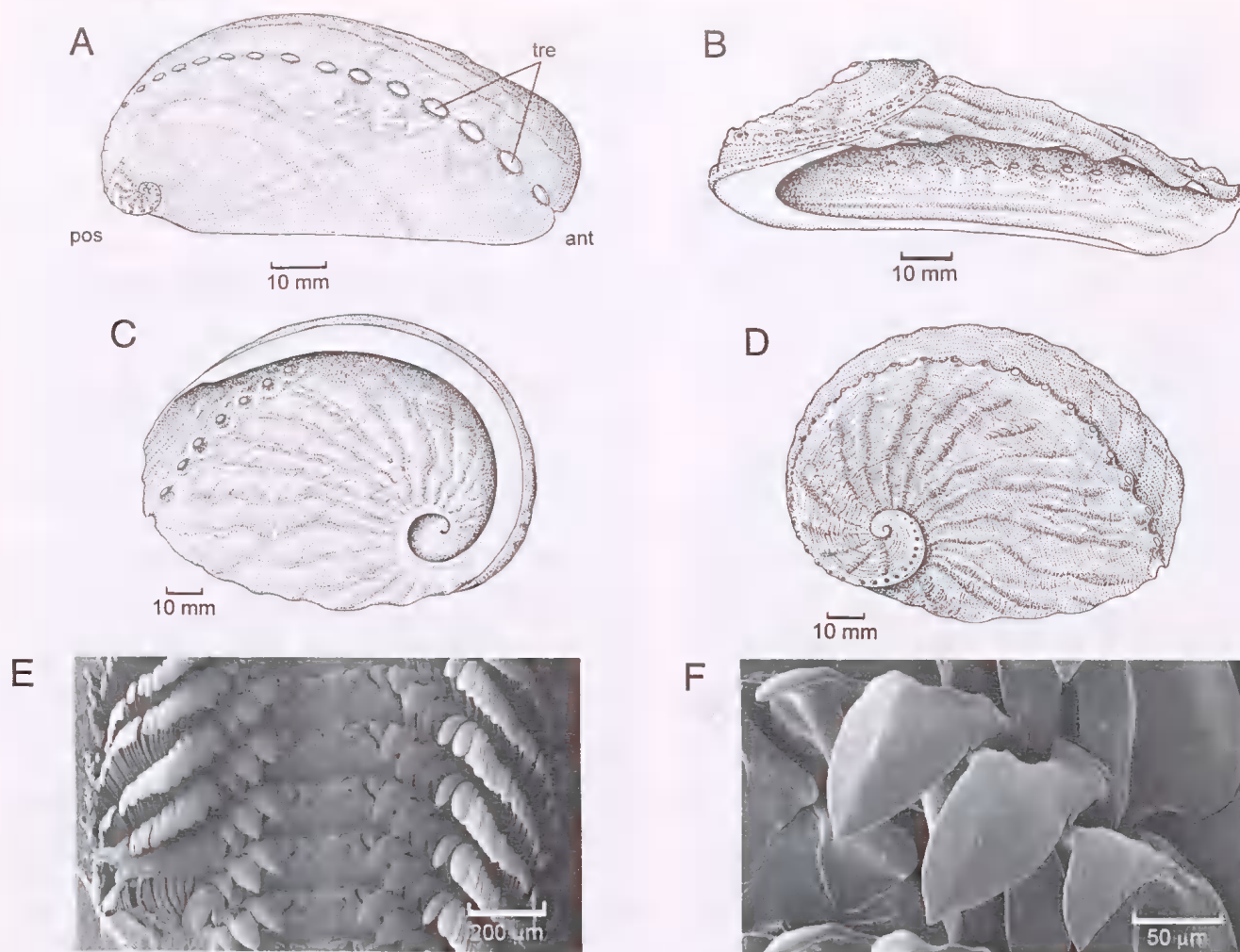


Figure 15.53 Family Haliotidae. A, *Haliotis asinina*, shell, dorsal view. B–D, *Haliotis ruber*, shell: B, apertural view; C, ventral view; D, dorsal view. E, F, *Haliotis rufescens*, from the north-eastern Pacific, portions of radula: E, mid-section showing all teeth across a few transverse rows; F, detail of the innermost marginal teeth showing the large interlocking cusps. ant, anterior; pos, posterior; tre, tremata. [A–D, S. Weidland; E, F, C.S. Hickman]

calcite and aragonite. Some of the smallest-shelled species reach a maximum length of less than 50 mm, whereas the largest may exceed 300 mm. The respiratory tremata range from nearly flush with the shell to elevated and anteriorly directed tubular chimneys. Old tremata are filled with aragonitic secretion from the surface of the mantle, but they remain visible on the exterior shell surface. The exterior shell surface may become heavily encrusted by red algae and other epizoans. Shells are commonly bored by sponges and bivalves while the animal is alive, and the secretion of 'blister pearls' is a common response to complete perforation.

The enlarged oval foot has an anterior notch through which the snout extends during feeding. The foot is capable of bursts of 'rapid' locomotion. Loss of the anterior pedal gland is an additional diagnostic character of the family. The dorsal surface of the foot may be papillate. Although the epipodium lacks neck lobes, cephalic lappets are present and the margin of the remaining epipodium is elaborated into sensory papillae and highly extensible tentacles of several lengths that project around the entire margin of the shell when the animal is active and not firmly clamped to the substratum. The cephalic tentacles are long, slender and highly extensible, and the eyes are situated on eye stalks that are better developed than in other extant pleuromarioideans.

The mantle is split over the dorsal roof of the mantle cavity, as in other pleuromarioideans, and the mantle edge can be enrolled into short, semitubular siphons that conform to the tremata in the shell. The edge is further elaborated into several sensory pallial tentacles that project from the tremata. The numbers and basic features of the pallial organs (ctenidia, osphradia, hypobranchial glands), heart, kidneys, gonads and nervous system are as described for the superfamily. The most detailed accounts of

haliotid anatomy and development are those of Crofts (1929, 1937). One of the most important treatments of haliotid ecology and development is Ino's (1952) detailed account of the Japanese species. A mimeographed translation of Ino's (1952) monograph by T. Kanaya is present in malacological reprint collections at many museums and academic institutions. Wells & Keesing (1989) and Keesing & Wells (1989) documented reproduction and growth in *Haliotis roei* in Western Australia and provided references to data from other haliotid species.

The haliotid radula (Fig. 15.53E, F) is of a strongly asymmetric rhipidoglossate form. The longitudinal axis of the radula does not bisect the rachidian, although the tooth itself is bilaterally symmetrical; and the right lateral teeth are situated anterior to the left lateral teeth on the radular ribbon (Fig. 15.53E). The inner two lateral teeth are relatively small, with short blunt cusps, and the three outer lateral teeth are greatly enlarged, with massive, sharply pointed cusps that are complexly interlocked (Fig. 15.53F). The asymmetry of the radula is an adaptation to accommodating mechanically the massive cusps during radular retraction (Hickman 1981a).

Diets of a number of species have been studied. Juveniles commonly settle on red algae and begin life feeding on microscopic surface films, although as adults they may feed either on living macroalgae or by trapping drift algae. Individuals may lift the entire anterior half of the foot off the substratum while trapping, which is accomplished by a combination of folding the foot around a trapped plant and subsequently clamping it to the substratum with the foot. Because they are primarily nocturnal feeders, this behaviour is seldom observed. Shepherd & Steinberg (1992) investigated the food preferences

of the three commercially important species in Australia and reported a preference for red algae and a low level of ingestion of the laminarian brown algae that are the preferred food of many species elsewhere in the world. Wells & Keesing (1989) have shown that the relative abundance of identifiable algae in the gut contents of *Haliotis roei* varies seasonally and between localities in Western Australia.

Many of the Australian haliotids are gregarious and occur at high population densities where they have not been exposed to heavy human predation. They are virtually restricted to firm or rocky substrata, occurring most commonly from the lowest part of the intertidal zone to depths of 15 m. They occur both in tropical and temperate waters, although they are most diverse and abundant on temperate Australian shores, where they also attain the largest shell sizes. The tenacity of the abalone foot is remarkable, although accounts of persons trapped by the clamping foot and drowned by the rising tide are apocryphal.

Abalone have been used for centuries as food and for jewellery and the fashioning of fish hooks. Shells occur in aboriginal middens. Australian abalone were dried and exported to China for a brief period in the late 19th Century (Tenison Woods 1882). However, the growth of a prosperous commercial industry, now worth more than A\$100 million annually, dates from 1965 (see also Chapter 1). Abalone fisheries in Australia concentrate on three of the relatively large-shelled species: the blacklip (*Haliotis ruber*), the greenlip (*H. laevigata*), and Roe's abalone (*H. roei*), and the main export markets are Japan, Malaysia, Hong Kong, New Caledonia, and the United States of America. Fisheries are managed independently by the State governments of New South Wales, Tasmania, Victoria, South Australia and Western Australia. Prince & Shepherd (1992) reviewed the biology of the three commercial species and the evolution of management practices in each of the five states. They also assessed the relative success of closures, size limits, and transferable individual quotas (TIQ's) as effective management measures. Poaching is an increasingly serious problem. As with many other commercially valuable mollusc species enforcement is a key issue.

The fossil record of haliotids dates back to the Upper Cretaceous in North America and to the Miocene in Australia. Ten species, distributed among four genus-group taxa (*Exohaliotis*, *Marinauris*, *Notohaliotis* and *Schizmotis*) occur in the Australian fossil record. Three of the ten species are extinct. Haliotids are uncommon as fossils, a reflection of the universally low frequency of burial of species from rocky shores and high-energy environments.

Superfamily FISSURELLOIDEA

Fissurelloideans, commonly called false limpets and keyhole limpets, form a derived group of vetigastropods that has acquired a limpet form, with a higher degree of secondary bilateral symmetry of the shell and mantle cavity than any pleurotomarioidean or trochoidean.

The operculum is not retained after metamorphosis and the anterior pedal gland is lost. The paired bipectinate ctenidia are of approximately equal size and are symmetrically situated. The shell and mantle have a notch, slit, or hole. The paired hypobranchial glands are reduced in size and confined to the region of the mantle adjacent to the slit or hole. There is no nacre. The shell structure is predominantly crossed-lamellar aragonite or complex crossed lamellar aragonite, sometimes with the addition of a thin outer calcitic layer in which pigment is deposited. Hypertrophy of the middle mantle fold is unique to the superfamily and may be accompanied by reduction or loss of the shell. Epipodial tentacles may be reduced or lost and epipodial sense organs are not so extensively developed as in most other vetigastropods. The left kidney is reduced to a vestigial structure, and the hypobranchial glands and the spiral gastric caecum are also reduced. Sexes are separate. Fertilisation is external, and larval development is lecithotrophic.

Fissurelloideans share primitive features with the less specialised pleurotomarioideans and more highly derived trochoideans. These include the diotocardian heart with two auricles of approximately equal size and a ventricle encircling the rectum; a hypoathroid, streptoneurous nervous system; paired osphradia; paired kidneys of differing size and function; and a single right gonad that discharges through the gonoduct into the renopericardial duct, which in turn joins the right kidney at its opening into the mantle cavity. Relative to the conditions seen in pleurotomarioideans and trochoideans the fissurelloidean left kidney is further reduced to a vestigial structure and both the hypobranchial glands and the spiral gastric caecum are reduced.

Until recently, this superfamily comprised the single family Fissurellidae. A second fissurelloidean family, Clypeosectidae, thus far known only from deep-sea hydrothermal vents is not treated separately here. The clypeosectid shell is characterised by an asymmetry of the slit or elongate foramen, the lack of shell pits or pores, and the absence of paired hook-shaped processes associated with the muscle scar. The animals lack eyes. The distinctive radula, first figured by Hickman (1983), differs in so many features from the equally distinctive radula of fissurellids that there are no radular synapomorphies to unite the families. Features of clypeosectid external anatomy, shell and radula are described by McLean (1989b), and features of internal anatomy by Haszprunar (1989b).

Family Fissurellidae

Members of this family are most readily distinguished from deep-sea clypeosectids by the bilateral symmetry of the shell and mantle cavity and the presence of distinctive shell pits, containing pores, canals, and chalky intritacalx, which are prominently developed on the early juvenile portion of the shell and may change in shape, orientation, and distribution during ontogeny if they continue on to the adult shell.

Fissurellids traditionally have been treated under three subfamilies (the Emarginulinae, Diodorinae and Fissurellinae) of the family Fissurellidae, although McLean (1984b, 1984c) recognised only two, the Emarginulinae and Fissurellinae, subdividing the former into three tribes (Emarginulini, Diodorini and Fissurellidini). Under McLean's classification, Fissurellidini is the only higher taxon not represented in the Australian fauna. Hickman (1981a, 1984c) summarised the major features of the fissurelloidean radula, and Herbert (1987a, 1988) and Herbert & Kilburn (1985) have provided excellent descriptions and illustrations of features of the shells, radulae and anatomy of many southern African species that are closely allied to species in the Australian fauna. The most comprehensive treatment of fissurellid anatomy is the detailed and meticulously illustrated early monograph of Boutan (1885). This work includes histology and an excellent account of development.

There is no comprehensive modern review of the family in Australia, although Cotton (1959a) listed most of the available names for Australian species. Approximately 66 fissurellid species are known from Australia, classified in 25 genera. Eleven of these genera are restricted to Australia, and five of these are monotypic. Genus-group taxa that are conspicuous in the Australian fauna include those that are cosmopolitan (for example, *Diodora*, *Emarginula* and *Puncturella*), those that are most prominently represented in Australia and New Zealand (for example, *Tugali* and *Montfortula*), those that are most prominently represented in southern Australia and southern Africa (for example, *Cosmetalepas* and *Macroschisma*, Fig. 15.54A) and those that are endemic to southern Australia (for example, *Amblychilepas*, Pl. 22.3).

The fissurellid shell (Fig. 15.54B–J) ranges in shape from nearly flat to steeply conical, with the apex of the shell curving posteriorly. Shell modifications for exhalant discharge range from a shallow anterior notch (for example, *Hemitoma*) or marginal slit with selenizone (for example, *Emarginula*) to a foramen located on the anterior slope (for example, *Rimula*) or apically (for

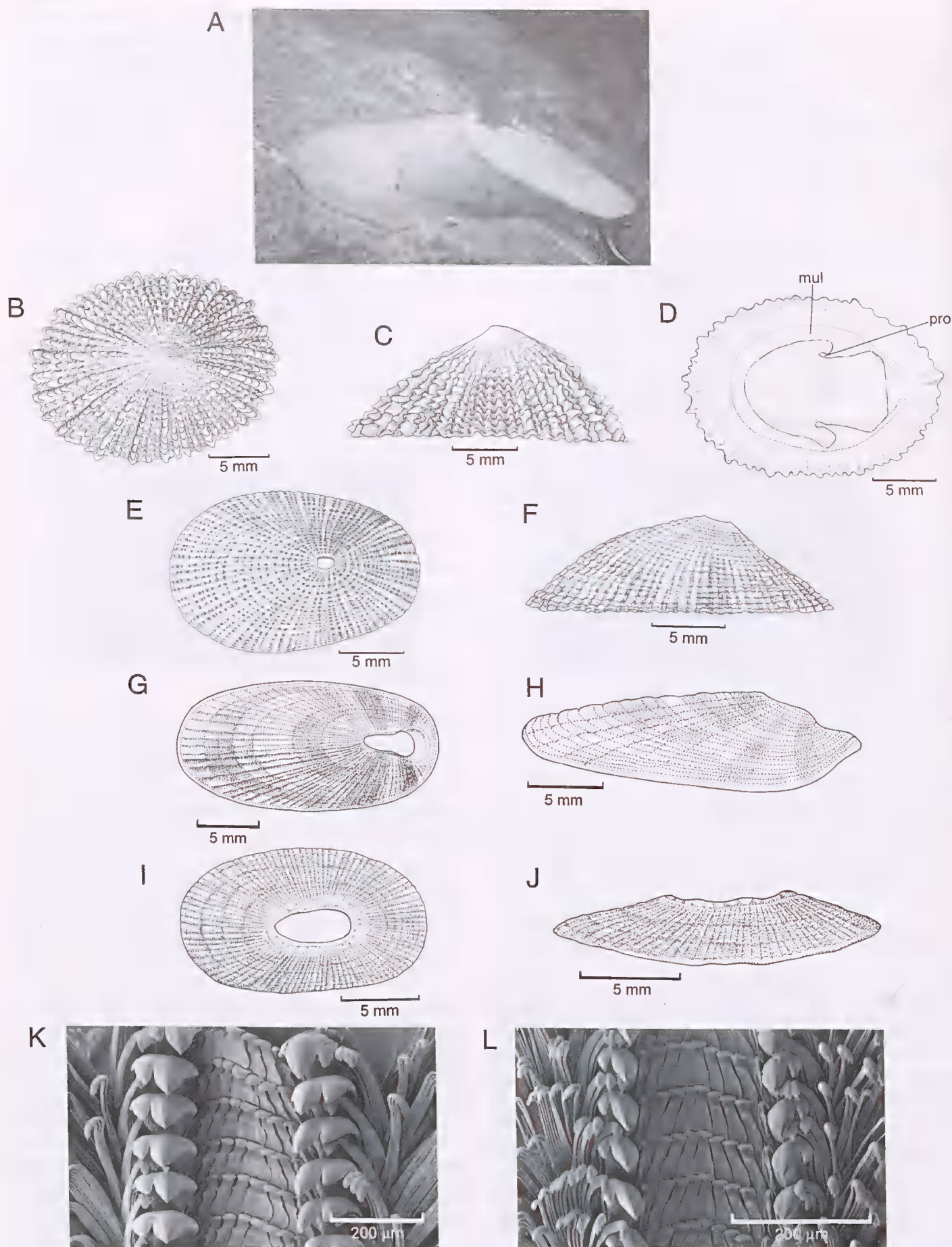


Figure 15.54 Family Fissurellidae. A, *Macrochisma producta* usually lives buried in sand under rocks in southern Australia; note the posteriorly directed exhalant siphon extending through the elongate foramen. B–D, *Montfortula conoidea*, a primitive emarginuline shell: B, dorsal view; C, lateral view; D, ventral view, showing the muscle scars on the shell interior. E, F, *Diodora lineata*, shell with a small apical foramen: E, dorsal view; F, lateral view. G, H, *Macrochisma producta*, shell with an enlarged foramen displaced posteriorly: G, dorsal view; H, lateral view. I, J, *Amblychilepas nigrita*, shell with a large central apical foramen: I, dorsal view; J, lateral view. K, L, portions of radulae: K, arcuately asymmetric radula of *Hemitoma octoradiata*; L, stepped asymmetric radula of *Montfortula rugosa*. B–F, I, J, anterior end of shell is to the right, and posterior to the left; G, H, anterior end of shell is to the left and the posterior to the right. mul, horseshoe-shaped muscle scar; pro, posteriorly directed process (scar) of muscle. [A, K. Gowlett-Holmes; B–J, S. Weidland; K, L, C.S. Hickman]

example, *Diodora*). A posterior internal septum occurs in some taxa (for example, *Zeidora*). The surface ranges from smooth to highly ornamented with radiating ribs or fine reticulate patterns. Intritacalx pitting is a prominent feature of emarginuline fissurellids, and Herbert & Kilburn (1985) presented a good summary of pitting patterns and how they develop. Shell colour ranges from white through a variety of pigments that commonly are deposited in a pattern of light and dark rays. Pigmentation only occurs in forms with an outer calcitic shell layer. The fissurelloidean protoconch is coiled and consists of approximately one whorl. The tip of the protoconch often shows the same mechanical deformation that is present in most trochoidean protoconchs. In taxa with an apical foramen (Fig. 15.54E–J), the hole is progressively enlarged by resorption of shell material by the outer mantle fold, and the inner mantle fold may be thickened and fused to form a posteriorly directed exhalant siphon (Fig. 15.54A). The muscle scars are joined posteriorly into a horseshoe-shaped scar that is open anteriorly. The primitive subfamily Emarginulinae has a pair of hook-shaped, posteriorly directed processes on each side of the muscle scar (Fig. 15.54D). The foot is enlarged and the mantle hypertrophied in many fissurellids, often with a concomitant internalisation and reduction of the shell. Shell reduction has occurred independently in at least three fissurellid clades. Two of the most common and striking fissurellids in the Australian fauna, *Scutus antipodes* (the black elephant slug) and *Amblychilepas nigrita* (the black keyhole limpet) have a shell (Fig. 15.54I, J) that is reduced relative to the size of the animal.

The large fissurellid foot often extends well beyond the posterior margin of the shell, and the sides of the foot are frequently covered with fine to coarse papillae. The propodium may be deeply bifid, with a snout protruding between the lobes. The epipodium is not complexly developed as in trochoideans, although a circlet of epipodial tubercles or even well-developed tentacles with basal epipodial sense organs may be present. The cephalic tentacles are stout, and the eyes are on short stalks or protuberances fused to the bases of the cephalic tentacles. There are no cephalic lappets or neck lobes.

The fissurellid mantle lobe has three distinct folds (Stasek & McWilliams 1973). In forms in which hypertrophy of the mantle is most extreme, the middle fold covers the narrow outer fold and extends upwards to cover the shell completely. The inner fold may be enlarged to cover the head and foot and thickened to form the roof of the mantle cavity in the absence of shell support. In forms with an apical foramen, the inner mantle fold may become thickened and partially fused to form a prominent exhalant siphon. Within the mantle cavity, there are paired, large bipectinate ctenidia, osphradia and hypobranchial glands. The pronounced reduction of the hypobranchial glands, which are characteristically large and convoluted in most vetigastropods, is characteristic of both fissurellids and clypeosectids. Filaments on each side of the central ctenidial axis are more or less symmetrical.

Features of the fissurellid heart, kidneys, gonads, and nervous system are as described for the superfamily. Fretter & Graham (1962) provided illustrations of many of these features, and references to a number of earlier accounts of fissurellid anatomy are given by McLean (1984b).

The snout is typically well developed, relatively short and broad, with a blunt tip that is sometimes expanded. Fissurellids have a distinctive radula (Hickman 1981a, 1984c) that is characterised by a suite of features including the relatively reduced development of the rachidian and four inner lateral teeth, the greatly enlarged and multicuspidate outer lateral tooth, the well-developed and distinctively faceted latero-marginal plate, and several characteristic forms of asymmetry that facilitate zipper-like accommodation of the enlarged outer laterals when the radula is retracted. Basic features of the fissurellid radula are illustrated in Figure 15.54K, L, which contrast the regular asymmetry of an Australian *Montfortula* species with the stepped asymmetry of the type species of *Hemitoma*. Additional suites of

radular features distinguish the two fissurellid subfamilies; radular asymmetry is more pronounced in the derived Fissurellinae. Gut contents indicate that many fissurellids are sponge-feeders or detritivores (Fretter & Graham 1962); although some species seem to be exclusively herbivorous, and others have been observed scavenging on animal material (Hickman unpublished data).

Sexes are separate and, as in trochoideans, there is considerable variation in spawning and patterns of development, including broadcast spawning and predominantly pelagic larval development, deposition of benthic egg masses that hatch either as veligers or as post-metamorphic juveniles. Some species brood their young (C.S. Hickman personal observation).

Many of the Australian fissurellids are restricted to the intertidal and shallow subtidal zones and all live on firm substrata. Although animals may be very common on the shore, they are less conspicuous than the true limpets because they tend to shelter in crevices, under rocks, or among other organisms. Fissurellids are often found among encrusting sponges. The Australian emarginuline species, *Montfortula rugosa*, is unusual because it extends up to mid-intertidal levels and is relatively common on exposed rocks within the cunjevoi and *Galeolaria* zones.

Although fissurellids are marketed as human food in some parts of the world (see McLean 1984b), their consumption in Australia has never been commercialised. Species diversity and generic diversity are both richest in the southern half of Australia. The low diversity in north-western, northern and north-eastern Australia is partly a reflection of the scarcity of rocky substrata and partly a reflection of the lack of a significant evolutionary radiation of the group onto carbonate reef substrata.

The family originated in the Triassic Period. Only the primitive subfamily Emarginulinae radiated during the Mesozoic Era; the Fissurellinae first appear in Eocene rocks. At least 45 fissurellid species are present in the Cainozoic rocks of Australia, including 27 extinct Tertiary species (Hickman unpublished data). Ornate emarginuline species are especially well preserved in the Neogene faunas of Victoria and South Australia. There are no extinct genus-level taxa in the Australian fauna as compared to 15 extinct genus-level taxa elsewhere in the worldwide.

Superfamily TROCHOIDEA

Trochoideans are more highly derived than the Plerotomarioidea and Fissurelloidea, typically having a conispiral shell that lacks a slit or emargination in the outer lip, which reflects the loss of the right ctenidium. The right osphradium is also lost. The epipodium is more complex, with flaps of tissue (neck lobes) that direct inhalant and exhalant currents through the mantle cavity. Epipodial tentacles are covered with sensory micropapillae and have simple or compound sensory macropapillae (epipodial sense organs) at their bases. The nephridial gland on the pericardial wall of the left kidney is unique to the Trochoidea. The rhipidoglossan radula has many specialisations related to food preparation, food collection, and mechanical interactions between teeth. The distinctive suites of radular characters provide the best synapomorphies for diagnosis of clades within the superfamily.

The most recent systematic revision of the superfamily (Hickman & McLean 1990) is based in large part on studies of the Australian fauna, and includes discussion and illustrations of many Australian representatives.

There are approximately 100 available generic names for trochoidean gastropods that are based on Australian type species. Twenty-eight of the best-known genera based on Australian material were described in Europe during the 19th Century (for example, *Phasianella*, *Stomatella*, *Monilea*, *Bankivia*, *Isanda*). Tom Iredale at the Australian Museum and Bernard Cotton at the South Australian Museum both had a special interest in Australian trochoideans and, during the first half of the 20th Century, described many genera and species from material housed in those

15. PROSOBRANCHS

institutions. Iredale proposed 40 trochoidean generic names and Cotton (with Godfrey) proposed 13. Laseon (1954a) introduced a number of names for minute liotiiform and skeneiform taxa, some of which are not trochoidean. Over the past two decades, Winston Ponder at the Australian Museum and Anders Warén at the Swedish Museum of Natural History, in the course of revising other microgastropod groups, have contributed further to the understanding of minute trochoideans.

Hickman (1995) discussed trochoidean phylogeny and evolution based on well-resolved cladistic analyses of the relationships of the nine turbinid subfamilies using 70 characters, and the 19 trochid subfamilies and tribes using 131 characters. The body of this paper is a narrative that defines characters and their states and presents criteria for their scoring.

There is considerable variation in the morphology of the trochoidean shell and operculum as well as in the external anatomy of the animal. This variation is summarised under the family and subfamily treatments that follow. The major features of the mantle cavity are conservative within the group (loss of the right ctenidium and osphradium, and retention of paired hypobranchial glands), but there is considerable variation in the morphology of the left ctenidium. It ranges from fully bipectinate to monopectinate, and a number of distinct grades of ctenidial evolution can be recognised within the group.

Major features of the trochoidean radula were characterised by Hickman & McLean (1990), who provided scanning electron micrographs illustrating the radular plans for all trochoidean subfamilies and tribes. The broad range of radular morphology in the superfamily is paralleled by a wide range of diets and feeding methods. Ontogenetic changes in trochoidean radulae are documented by Warén (1990), who has shown that in the radiation of the Trochoidea, the variation in adult radular morphology derives from a common juvenile groundplan.

Internal anatomy is conservative throughout the superfamily and differs little from that of pleurotomarioideans (Fretter 1964, 1966). Fretter & Graham (1962) and Graham (1965b) described and illustrated the basic features of trochoidean anatomy and referred to earlier anatomical studies. Although they emphasised the basic similarity of internal anatomy across the group, representatives of many of the trochoidean lineages have not yet been examined anatomically (Hickman & McLean 1990).

Anatomical features that are shared with the less apomorphic pleurotomarioideans and more highly derived fissurelloideans were reviewed by Hickman (1995). The heart has two functional auricles (diotocardian) and a ventricle encircling the rectum. The nervous system has a hypoathroid anterior nerve ring and a streptoneurous visceral loop. The functional anatomy of the trochoidean excretory system was discussed and illustrated by E.B. Andrews (1985, 1988). The kidneys differ in size, structure and function. The right kidney is large and deals primarily with nitrogenous waste. The smaller left kidney is filled with papillae that project into the lumen, and appears to function in the regulation of water, ion concentrations, and possibly of other substances in the blood. The left kidney in trochoideans is large relative to the vestigial condition in fissurelloideans, and the presence of the so-called 'nephridial gland' is unique to this superfamily. There is a large, distinctive, spiral caecum as in pleurotomariids and haliotids. Beneath the dorsal folds and food channel of the mid-oesophagus, the epithelium is elaborated into complex glandular folds and papillae that extend into pouches on each side of a prominent ventral fold. A single right gonad is present and gametes pass first through a duct of gonadal tissue to a renopericardial duct that joins the anterior end of the right kidney and finally into the mantle cavity through glandular mantle tissue (a short, open pallial gonoduct) that may be elaborated as a large papilla in females (Hickman 1992). This feature is illustrated in the mantle cavity dissection of the Australian species, *Prothalotia lehmanni*, by Hickman (1992).

Trochoidean reproduction and development were reviewed by Hickman (1992). The sexes are separate and fertilisation is external. Sperm are of the primitive ect-aquasperm type, but with some remarkable deviations within several trochoidean clades. Eggs may be broadcast into the water column, discharged as strings, or fixed to the bottom as benthic masses. Brooding has developed independently in several groups. Cleavage follows the classic spiral molluscan pattern, and gastrulation is by epiboly. Trochophore and veliger stages are present, but the stage at hatching ranges from the early trochophore to the juvenile, following metamorphosis. Although planktonic larvae have a limited ability to delay settlement and metamorphosis and can spend up to several weeks in the water column, no trochoidean veligers are known to feed. This is reflected in the trochoidean protoconch, which typically has a large initial whorl with few post-nuclear whorls and no prominent morphological discontinuity between the pre- and post-hatching portions. In all of these features, trochoideans differ little from other vetigastropods.

Life histories are known for very few species and range from species that complete their life cycle in one year to some that live for greater than ten years. Gametogenesis and spawning may be continuous or periodic; both patterns can be found in sympatric congeners and spawning may follow tidal, daily, and lunar cycles. Epidemic spawning and aggregation or pairing of individuals occurs in some species. Life history data have been summarised by Hickman (1992).

Trochoideans occur in most marine habitats and on a wide variety of substrata. In Australia, they are conspicuous or dominant members of some rocky intertidal communities (for example, *Austrocochlea*, *Monodonta*), high-energy sand substrata near wave base, (for example, *Bankivia*), low-energy intertidal sand flats (for example, *Isanda*), and in a variety of marine plant communities (for example, cantharidine species and *Tricolia* on various seagrasses and brown and red algae). They constitute an important food source for some fish and birds, and evidence of breakage and subsequent repair to the growing shell margin is common in many species. Some taxa have close interactions with other organisms (for example, species of *Euchelus* that are encased in sponge and species of *Calliostoma* that are consistently associated with the cnidarian or sponge species on which they feed).

Many species are negatively phototactic, spending the daylight hours under rocks. Typically they are highly active animals that right themselves and resume their preferred orientation rapidly when disturbed, and the patterns of righting behaviour are stereotyped and clade-specific (C.S. Hickman personal observation). During locomotion, the cephalic and epipodial tentacles wave actively and are touched frequently to the substratum. Waving of the epipodial tentacles exposes the epipodial sense organs at their bases and may function in regulation of flow over the epipodium (C.S. Hickman personal observation). Species that graze surface films on rocks and plants may spend considerable time feeding while moving, executing 30 or more feeding strokes per minute.

The beauty of the trochoidean shell pigmentation patterns and of the underlying nacreous shell layer has promoted use of some species in Australian folk art (for example, the use of *Bankivia* shells in necklaces and as weights on the edges of doilies used to exclude flies from milk jugs; Hickman unpublished data). *Trochus niloticus* shell is the basis of a profitable Australian fishery (see also Chapter 1). *Trochus* species are also common in some aboriginal middens (C.S. Hickman personal observation).

Australia is the major centre of living trochoidean generic and species diversity. The major trochoidean families, Turbinidae, Trochidae and Skeneidae, are well represented in the fauna. The Pendromidae are represented in the Australian fauna by an undescribed species from deep water. Of the 22 subfamilies recognised by Hickman & McLean (1990), only five are not represented in Australia. Eight of the subfamilies are represented by endemic genera and species groups that have undergone significant Cainozoic radiations in Australia and New Zealand. The relationship of the trochoidean faunas of Australia and New Zealand is poorly

understood. Marshall's (1979) account of 30 trochid and turbinid species from the Kermadec Ridge emphasises the strong endemism and lack of faunal connections. The distinctive Tertiary trochoidean fauna of New Zealand is preserved in a more complete stratigraphic sequence than that of Australia and has been studied more intensely; there are approximately 170 named trochoidean species. Data on this fauna are contained in the compilation and illustration of New Zealand fossil molluscs by Beu & Maxwell (1990).

Trochoideans are well represented in the faunas of the Tertiary basins of Victoria, South Australia and Western Australia. More than 100 named species occur in the Tertiary, and there are many undescribed species, especially in Eocene beds (C.S. Hickman personal observation). Quaternary fossil deposits also contain many trochoideans. Few Quaternary species are extinct, although a number of species occur in deposits outside the geographic range of the living populations (C.S. Hickman personal observation).

Until recently, most Australian trochoideans (including some of the most common species in the fauna) were known only from shells; details of anatomy and habitats of the animals are unknown. Washings of marine algae and dredging of clastic substrata using finer mesh dredge liners have been especially productive of new species and live material of species previously known only from empty shells. Bulk sampling, disaggregation, and screening of Tertiary sediments is the primary source of undescribed fossil taxa. Epipodial features cannot be interpreted properly from preserved specimens. Live animals should be observed, drawn, and/or photographed as soon as possible after collection. Most small individuals respond well to relaxation with magnesium chloride before formalin fixation. The shells of large specimens should be cracked to ensure proper fixation. Methods of study of the trochoidean radula are described in a series of papers by Hickman (see Hickman & McLean 1990 and references therein).

Family Turbinidae

Turbinids are characterised by the partially or fully calcified operculum and by a series of novel radular features. The operculum has a long growing edge. The radula has a broad oval rachidian tooth that lacks a distinct shaft and double cusp; a secondary flap provides additional attachment to the radular membrane. The five pairs of lateral teeth have a characteristic bend in the shaft, which expands into bases with a distinctive pattern of overlapping and interlocking. Traditionally the family has been restricted to taxa with a sturdy shell and the familiar convex calcified operculum commonly described as a 'cat's eye', whereas the Liotiidae (wheel shells), Angariidae (dolphin shells) and Phasianellidae (pheasant shells) have been treated as distinct trochoidean families, both in Australia (for example, Cotton 1959a) and elsewhere. On the basis of shared radular features, Hickman & McLean (1990) expanded the diagnosis of the family and reduced the traditional family units to subfamily status as a means of expressing their relationships to one another.

Turbinid shells are usually thick and sturdy, with an aperture that is circular, uninterrupted and nearly radial in the primitive state, becoming ovate, interrupted and prosocline in the more highly derived subfamilies. The operculum is multispiral in the primitive groups and paucispiral in the derived ones, where it also becomes partially enveloped by the metapodium.

The epipodium is relatively unspecialised and lacks cephalic lappets in the primitive subfamilies. In the derived subfamilies, the neck lobes are broader and subdivided in a complex manner. The afferent membrane of the ctenidium is primitively short, but more elongate in the derived subfamilies.

In some of the derived turbinids, the snout is split mid-ventrally and drawn out into a pseudoproboscis, a structure of unknown function. Members of the family are most common on calcium carbonate substrata and many ingest calcium carbonate with their food. A number of clades are associated consistently with red coralline algae either as juveniles or adults (C.S. Hickman personal observation).

Two of the nine turbinid subfamilies, both erected by Hickman & McLean (1990), do not occur in Australia. Moelleriinae are restricted to high latitudes in the Northern Hemisphere, and Prisogasteriinae are restricted to the Peruvian province of South America. A third subfamily, Colloniinae, is represented in Australia by a single, poorly known genus, *Collinista*, and is not treated separately here. The other six subfamilies (Liotiinae, Angariinae, Turbininae, Gabrieloninae, Tricholiinae and Phasianellinae) are well represented both in the living Australian fauna and in the Cainozoic fossil record and are sufficiently diverse in morphology and ecology that they are treated individually. Their separate treatment also recognises that many authors may wish to accord some or all separate familial status. Hickman (1995) has analysed the phylogenetic relationships of the turbinid subfamilies.

Subfamily Liotiinae

The Liotiinae are the most primitive subfamily of the Turbinidae. Liotiines are diagnosed by the presence of a calcified periostracum on the shell, which is sculptured with distinctive scaly axial lamellae between the primary spiral and axial ribs, as well as prominent thickening of the outer lip and the presence of calcareous granules on the exterior surface of the operculum.

Fifteen Australian species, in seven genera, are relatively common and well represented in the major museums in Australia. Some of the species names based on Australian specimens are synonyms. Cotton (1959a) listed many of the available names. The three most common genera in Australia are *Austroliotia*, *Liotina* and *Pseudoliotina*. The minute-shelled liotiine species are poorly known for a combination of reasons. The habitats in which they occur are infrequently or inadequately collected to retain the fine fraction, and sorted specimens are frequently misidentified.

The Liotiinae often have been treated as a distinct trochoidean family by Australian authors (for example, Laseron 1954a), and have included a diverse assemblage of minute-shelled forms that are treated under Skeneidae or Cyclostrematidae in other classifications. Laseron (1954a) based ten new generic names on Australian minute-shelled species and extended the concept of the family to include a number of taxa that lack apertural thickening and the fringed, granulated operculum. Following Laseron, Cotton (1959a) included the microlotiiform (with apertural thickening) and skeneiform (without apertural thickening) taxa in a concept of the Liotiidae that included the Colloniinae, Skeneinae and Cyclostrematinae as subfamilies. Jenkins (1984a, 1984b) reviewed the Australian species of *Austroliotia*, *Munditia*, *Lodderena*, *Liotina*, *Pseudoliotina*, *Dentarene* and *Circumstella*. Hickman & McLean (1990) provided a revised characterisation and historical review of the subfamily.

The liotiine shell (Fig. 15.55A) is small (typically less than 10 mm), relatively thick, and usually unpigmented, with a circular aperture that is not interrupted and is nearly radial. Interior nacre is usually inconspicuous. A ragged corneous fringe that develops along the margin of the round, multispiral operculum as it grows may partially or fully obscure the calcareous granules that are secreted in a radiating pattern on the outer surface. Opercular retraction is shallow (Fig. 15.55A).

The external anatomy of a typical liotiine animal is illustrated in Figure 15.55B. The foot is small, and does not extend over the base of the shell when the animal is resting or crawling. The epipodium is relatively simple, with a poorly differentiated, tentaculiform neck lobe, three or four pairs of short epipodial tentacles and no cephalic lappets. The single ctenidium is bipectinate along three-fifths of its length and the short dorsal afferent membrane is restricted to the region posterior to the transverse pallial vein.

The tubular snout is short and relatively broad; the radula is turbinid in plan and is symmetrical in its development (Fig. 15.55C). The central and marginal tooth fields are equally well developed and there is no enlargement of the inner marginal tooth cusps. The secondary rachidian cusp is well developed in

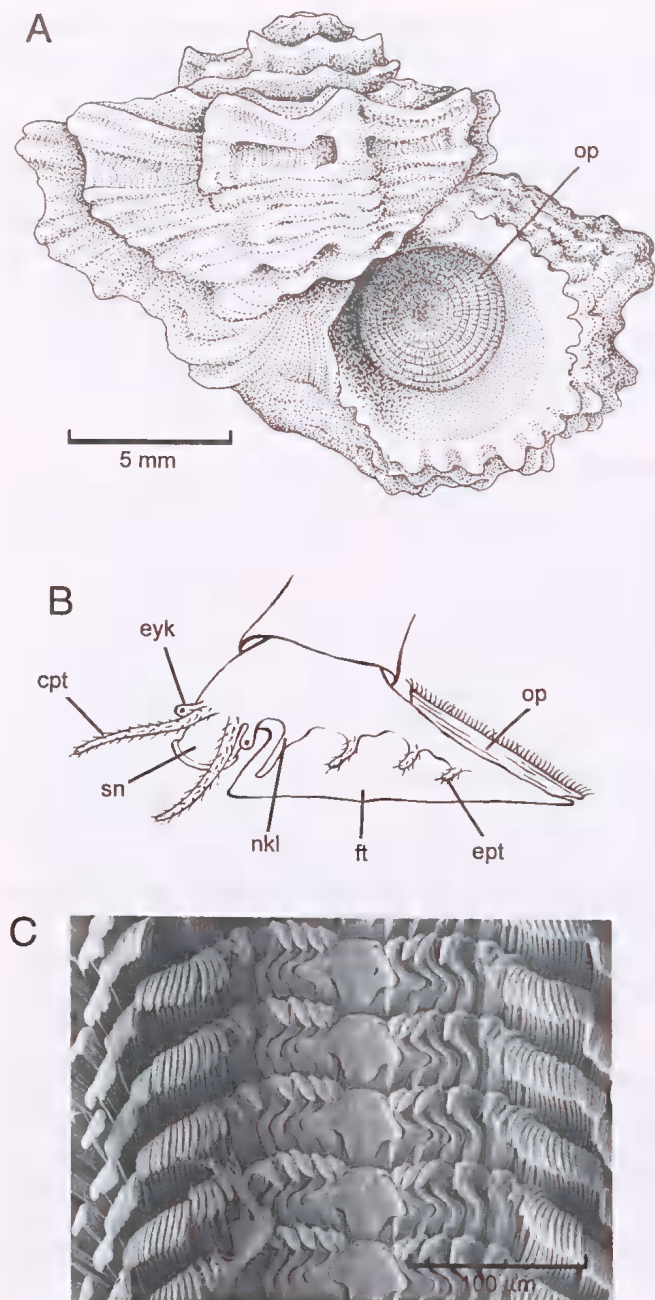


Figure 15.55 Family Turbinidae, subfamily Liotiinae. A, *Liotina peronii*, shell with operculum, apertural view. B, *Macarene cookeana*, from Baja California, external features of head-foot. C, *Arene hindsiana*, from Mexico, mid-section of radula showing most teeth across several transverse rows; note the characteristic bend in the shaft of the lateral teeth. cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; sn, snout. [A, S. Weidland; B, M.E. Taylor; C, C.S. Hickman]

many species. The innermost marginal tooth shaft is expanded into a proto-latero-marginal plate, and a prominent food groove is formed by notches beneath the cusps of the marginal teeth. Feeding behaviour and diet have not been documented.

Members of the subfamily occur around the entire Australian coastline over a range of depths from the intertidal zone to the edge of the continental shelf. They are commonly associated with rocky or rubbly substrata. Individuals can be relatively common under rocks on intertidal reef platforms. Animals are active at night, and seek refuge under rocks by day. Burn (1976) illustrated an individual of the Australian species *Munditia subquadrata* with a mass of developing embryos in the umbilicus; this is the only report of brooding in the subfamily (Hickman 1992).

The subfamily originated in the Permian and its fossil record in Australia extends back into the Eocene. Several Victorian Pliocene species are abundant and extremely well preserved.

Subfamily Angariinae

Members of the primitive subfamily, Angariinae, share many features with the other primitive subfamily, Liotiinae. They are distinguished by the lack of any form of calcification of the operculum, which is completely corneous, and by the development of pronounced radular asymmetry, reduction in the size of the rachidian and inner lateral teeth, and pronounced enlargement of the outer lateral and inner marginal tooth cusps. Elaborately branched spines are produced in some deep-water taxa.

The so-called dolphin shells are represented by a single extant genus, *Angaria*, and in Australia by the broadly distributed Indo-Pacific species, *A. delphinus*, and a number of other forms for which species names are available. The name *Angaria tyria* commonly is applied to populations between Cockburn Sound and North West Cape in which spines are lacking or poorly developed. Other names based on Australian specimens (see Cotton 1959a), such as *Angaria incisa*, are of dubious status: they were proposed for colour variants or spine forms. Local populations do tend to be distinct in spine morphology and ornamentation, which may be related to local variation in diet (C.S. Hickman personal observation). There also may be considerable variation in shell form and ornamentation within populations (C.S. Hickman personal observation).

This subfamily traditionally has been classified under the Trochidae or as a distinct family (Angariidae or Dephinulidae) by authors who have noted unique shell features and lack of opercular calcification, but failed to note the modified turbinid radular plan. Cotton (1959a) is among the Australian authors who have accorded familial status to the group. Hickman & McLean (1990) have provided an illustrated revised diagnosis of the subfamily that includes scanning electron micrographs of the radulae of Australian specimens.

The angariine shell (Fig. 15.56A) is of medium to large size (for example, up to 60 mm high and 70 mm wide for *Angaria delphinus*) relative to that of liotiines, with which they share the nearly radial, circular aperture with an uninterrupted margin. They lack the liotinine terminal thickening of the aperture, although the margin is frequently expanded or flared. Sculpture, shell thickness and colouration may be highly variable from one population to another. The most spectacular shells, occurring in deeper water, are ornamented with imbricate scaliform axials and intermittently secreted semitubular spines. Spines and spine branches are secreted by sharp folds in the mantle. They are always hollow and show a trace of the meeting of the folds of the mantle on the anterior surface: most are open on the side facing the aperture and appear as tightly folded structures. This is one of the few trochoidean groups in which disjunct coiling of the shell develops in some individuals. Opercular retraction is unusually deep, in contrast to the shallow opercular retraction of liotiines. The operculum is multispiral, as in liotiines; and the foot is short and does not expand to cover the base of the shell.

The head-foot is illustrated in Figure 15.56B. The epipodium is relatively unspecialised and lacks cephalic lappets as in the Liotiinae. There are three pairs of epipodial tentacles. The neck lobes are narrow, with simple margins, but are slightly more elaborate in the addition of short projections from the anterior and posterior ends of the left neck lobe. The ctenidium, like that of liotiines, has a primitively short dorsal afferent membrane.

The major features of the angariine radula are illustrated in Figure 15.56C. The characteristic asymmetry functions to accommodate a unique pair of enlarged outer lateral tooth cusps when the radula is retracted and enroled (Hickman 1981a). The marginal teeth have unusually long overhanging cusps with rounded tips. The enlarged two outer lateral teeth are of a distinctly different form from the three small inner laterals, with a unique overlapping and interlocking of the cusps in the region where they are joined to the shaft. The arrangement of cusp enlargement and interlocking found in the subfamily Turbininae (Hickman 1984c), in which the inner pair of marginal teeth rather than the outer pair of laterals

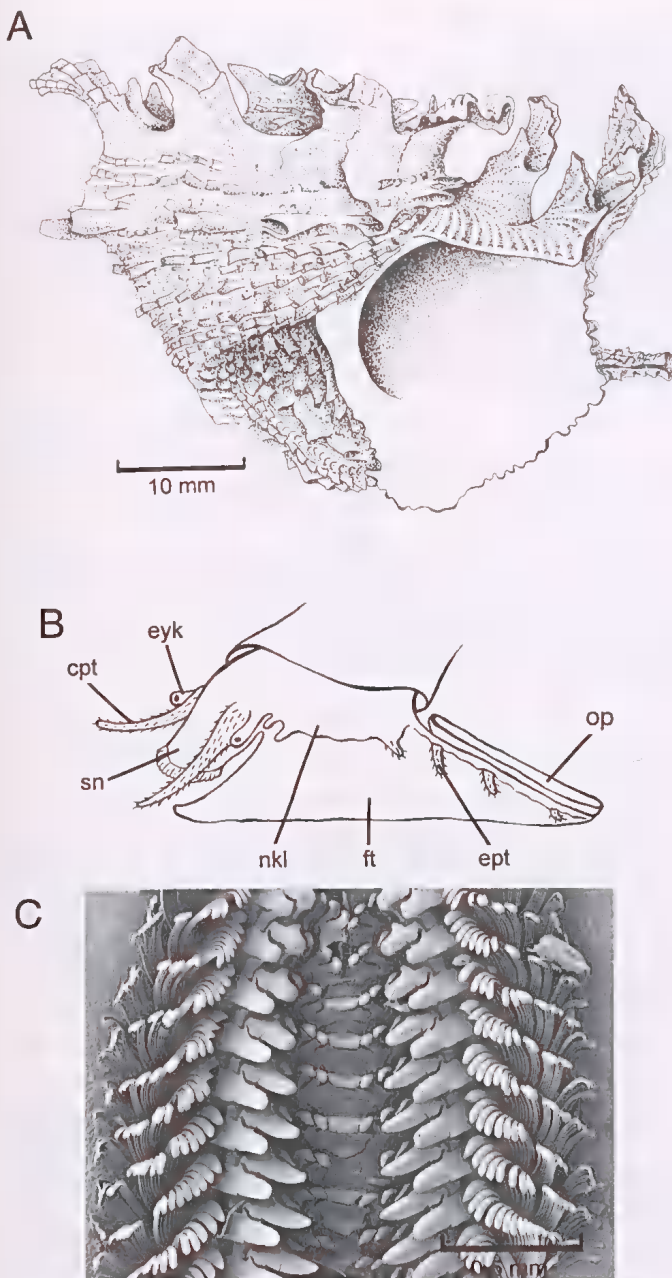


Figure 15.56 Family Turbinidae, subfamily Angariinae. *Angaria delphinus*: A, shell, apertural view; B, external features of head-foot; C, mid-section of radula, showing all teeth across several transverse rows. *cpt*, cephalic tentacle; *ept*, epipodial tentacle; *eyk*, eye stalk; *ft*, foot; *nkl*, neck lobe (left); *op*, operculum; *sn*, snout. [A, S. Weidland; B, M.E. Taylor; C, G. Avern]

has been modified, has developed independently; the pattern of interlock differs (see Fig. 15.57D, Turbininae).

This subfamily is tropical and subtropical in its Australian distribution. It occurs typically on rock substrata. Although it is also found on what appears to be coral sand (as in the Houtman Abrolhos), the foot will often prove to be attached to a slab or coral or larger piece of subsurface coral rubble. The genus *Angaria* does not occur on the southern coast of Australia today, although it does occur in the Tertiary basins of the south coast.

Like liotiines, angariines have a long fossil history. They first appear in the Jurassic, and in Australia they are known from the Cretaceous to the Holocene. At least three extinct species of *Angaria* (*A. imparigranosa*, *A. gibbuloides* and *A. tetragonostoma*) occur in Australian Tertiary basins, and Darragh & Kendrick (1994) have described a new species of the extinct genus *Nododelphinula* (*N. dracontis*) that is common and often well preserved in the Upper Cretaceous Miria Formation in north-western Australia.

Angariines are difficult to relax prior to fixation because they tend to remain withdrawn into the shell. The shells of large specimens should be cracked for successful fixation and preservation.

Subfamily Turbininae

The Turbininae include the genera and species commonly known as turban shells, tent shells and star shells. In contrast to members of the primitive subfamilies Liotiinae and Angariinae, turbinine gastropods have a shell aperture with an interrupted peristome and an operculum which is embedded in the metapodium and has a calcified outer surface, a more complex epipodium that includes cephalic lappets, and a ctenidium with a long dorsal afferent membrane.

Turbinine gastropods are a conspicuous element in the Australian intertidal fauna and are among the most sought-after trochoideans for shell collections, ornaments and food. The operculum is more resistant to destruction than the shell and has different hydrodynamic properties, leading to frequent concentrations of opercula in rock pools and beach drift. More than 75 names have been applied to species in the Australian fauna. Most of the available names were listed by Cotton (1959a).

Eleven genus-group names have been proposed for species that are endemic to Australia or have broader distributions that include Australia. Four genus-level taxa allied with *Turbo* (*Carswellina*, *Dinassovica*, *Euninella* and *Subninella*) are endemic to Australia, and two genus-level taxa allied with *Astrarium* (*Bellastraea* and *Micrastraea*) are endemic to Australia. Beu & Ponder (1979) reviewed the living and fossil Australian species of *Bolma* and Underwood (1974) and Joll (1980) provided accounts of the reproductive biology of three common temperate intertidal species of *Turbo*. A separate turbinid subfamily, the Astracinae, is sometimes considered for some taxa. Hickman & McLean (1990) revised and illustrated the subfamily diagnosis and summarised the historical treatment of the group, and Hickman (1992) reviewed the knowledge of reproductive biology and development relative to other trochoideans.

The shells (Fig. 15.57A, B) are thick, with surfaces that range from smooth, lustrous and brightly coloured to coarsely nodose, scaly or spiny, with subdued colour patterns. The parietal callus is frequently well developed, spreading over the columella and a portion of the base of the shell. The round or oval, exteriorly convex, calcareous ('cat's eye') operculum is frequently bright green, blue or orange. The operculum ranges from strongly sculptured (Fig. 15.57A) to smooth (Fig. 15.57B). The juvenile shell is typically strongly bicarinate. Adult shells are usually globose (Fig. 15.57A) except for the star shells (*Astrarium*), which are conical with flat bases (Fig. 15.57B). Some of the deep-water turbans have delicate spines, although the most elaborately spinose species occur subtidally in the more tropical Indo-Pacific. Adult shell size of Australian members of this subfamily ranges from 12 mm high in *Carsellena exquisitus* to 200 mm high in *Dinassovica jourdani*, the largest Australian trochoidean.

Features of external anatomy are illustrated in Figure 15.57C. The epipodium is intermediate in elaboration between that of the more primitive Liotiinae and Angariinae and the more highly derived turbinid subfamilies. Cephalic lappets are present and the neck lobes are broader, although they have simple margins. Epipodial tentacles are short and stubby. The snout terminates in a broad oral disc and the lip is split mid-ventrally and extended to the left into a well-developed pseudoproboscis of unknown function.

All species are herbivorous and live on rocky platforms, predominantly on calcium carbonate substrata. The radula (Fig. 15.57E) is of the typical turbinid plan, but it is strongly asymmetric with relatively reduced rachidian and lateral teeth (five per half row) in contrast to the enlarged, strongly cuspidate inner marginal teeth. A few taxa retain an overhanging cusp on the rachidian tooth (Fig. 15.57D). Frequently the enlarged cusps of the innermost marginal teeth have a secondary cusp that overlaps and fits into a shallow depression at the top of the primary cusp on

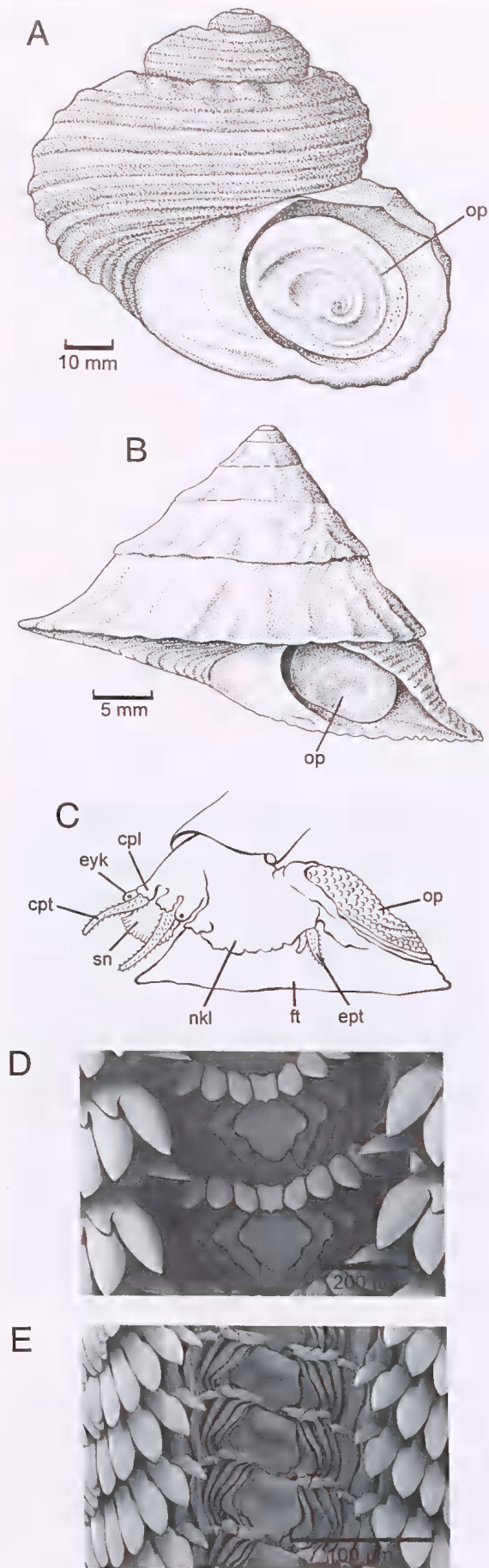


Figure 15.57 Family Turbinidae, subfamily Turbininae. A, *Turbo torquatus*, globose shell with sculptured operculum, apertural view. B, *Astralium tentorium*, conoidal shell with smooth operculum, apertural view. C, *Turbo fluctuosus*, external features of head-foot. D, E, portions of radula: D, *Turbo smaragdus*, central field of two transverse rows; E, *Astraea heliotropium*, several transverse rows. cpl, cephalic lappets; cpt, cephalic tentacles; ept, epipodial tentacles; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; sn, snout. [A, B, S. Weidland; C, M.E. Taylor; D, E, G. Avern]

the adjacent tooth (Fig. 15.57D, E); see Hickman (1984c) for further discussion on cusp overlap and interlocking and biomechanical significance.

Spawning has not been observed in the field, and attempts to induce spawning or to fertilise eggs artificially and rear larvae have failed (Underwood 1974; Joll 1980). However, seasonal sampling and histological examination of gonads showed continuous gametogenesis with one or more peaks in the proportion of mature oocytes, which probably preceded discrete spawning events. Benthic egg masses have not been reported for any of the Australian species, although both broadcast spawning and benthic deposition of eggs are known in the group from elsewhere (see Hickman 1992 and references therein).

The ecology of the Australian species is poorly documented, which is surprising since they are among the largest and most abundant herbivores in the low intertidal zone on many shores and might be expected to influence community structure. Outside Australia, several turbinine species have been shown to occupy different substrata as juveniles and adults (see for example, Walsby 1977), and to change the pattern of shell secretion in response to changes in diet (see for example, Ino 1953). For a summary of studies on the ecology of Australian turbinids, see Worthington & Fairweather (1989) and references therein.

Although turbinines are no longer taken commercially in Australia, a small pre-war fishery in Queensland and the Northern Territory was based on the green snail, *Turbo marmoratus*, which was used primarily in the manufacture of mother-of-pearl buttons. A small, Tasmanian commercial fishery is based on *Turbo undulatus* (see also Chapter 1). The operculum of the cat's eye turban, *Turbo petholatus*, has been used extensively in jewellery. Although turban snails are not fished on a commercial scale for food, shells of several of the temperate species are abundant in aboriginal middens and the snails are still eaten by a number of Australian communities.

The subfamily occurs around the entire coastline of Australia, although there are distinct tropical and temperate taxa. Species can be divided into those with broad ranges in the tropical northern Australian region, those with broad ranges in the temperate southern Australian region, and those that are endemic to small segments of the coastline. Species of *Turbo* (and its subgenera) and *Astralium* are predominantly intertidal to shallow subtidal, whereas those of *Bolma* and its allies are predominantly offshore in deeper water. Very large shells are not restricted to the tropical forms. For example, *Turbo torquatus*, one of the commonest turbinids of temperate rocky coasts, is also one of the largest gastropods on Australian seashores, with adult shells typically exceeding 100 mm.

Both the globose turban and the conical tent shells have a good fossil record in Australia beginning in the Eocene. Fifteen extinct Australian species have been described under seven generic names. There are at least two undescribed species in museum collections, including specimens of a large Miocene *Dinassovica* that reaches 225 mm in height (C.S. Hickman personal observation). A number of the living species are represented in Pleistocene marine terraces by abundant well-preserved shells and opercula (C.S. Hickman personal observation).

The large turban are difficult to relax prior to fixation and frequently retract into the shell so that the animal is sealed off by the tight-fitting operculum. Cracking of the shell is essential for successful formalin fixation.

Subfamily Gabrieloninae

This subfamily is diagnosed by the presence of a distinctive apertural ridge and a palatal sulcus on the interior of the shell and by an operculum that is exteriorly concave and has a bordering ridge except where it fits against the columella. The palatal sulcus (Robertson 1973b) is a narrow, shallowly incised furrow on the shell interior that typically is located beneath a spiral element of the pigmentation pattern on the shell exterior.

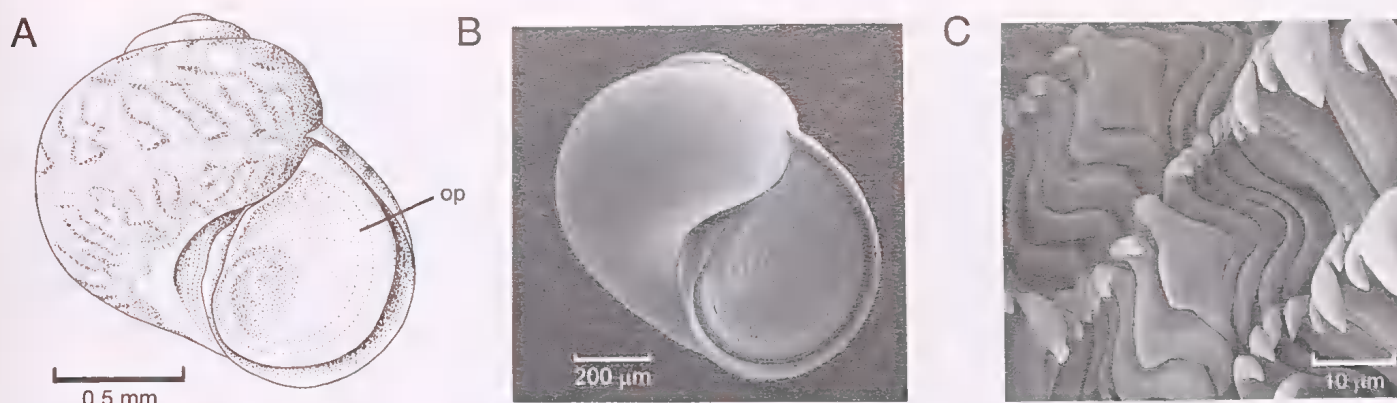


Figure 15.58 Family Turbinidae, subfamily Gabrieloninae. A, B, *Gabrielona pisinna*: A, shell showing the typical pigmentation pattern, apertural view; B, shell with concave operculum. C, *Eugabrielona sulcifera*, from Mexico, several transverse rows of radular teeth showing the rachidian tooth, the interlocking lateral teeth and the inner marginal teeth with large cusps. op, operculum. [A, S. Weidland; B, C, G. Avern]

Of the two genera in this small subfamily, only *Gabrielona* is present in Australia, represented by the endemic *G. neapeanensis* (the type species), and the endemic, *G. pisinna* (Fig. 15.58A, B), and possibly several undescribed species. Robertson (1973b) reviewed the genus and subsequently noted (Robertson 1985a) that it is not closely related to the other species that have been treated as 'pheasant shells' under Phasianellinae or Phasianellidae. Hickman & McLean (1990) recognised it as a distinct clade within Turbinidae.

The shell of *G. neapeanensis* is minute (less than 2 mm high), globose and thin, with a translucent spiral band on the surface corresponding with the interior palatal sulcus. There are two small columellar denticles. There is no visible interior nacre, and the pigmentation pattern is highly variable, with a predominance of pink and white pigments deposited in wavy or zigzag stripes or as irregular blotches. The most distinctive features of the thin, translucent white operculum are its external concavity and the thin spiral ridge near the outer edge. The shell and operculum of *G. pisinna* are illustrated in Figure 15.58A, B.

Almost nothing is known of the internal anatomy, or external features of the animal of this subfamily. Radulae have been extracted from dried animals and show considerable variation in morphology (Robertson 1973b; Hickman & McLean 1990). The radula illustrated in Figure 15.58C has a typically turbinid rachidian tooth with an ovate base and without a distinct cusp, and has the characteristic interlocking lateral teeth with a mid-shaft bend that fits into a pocket on the adjacent tooth. The enlarged inner marginals have thick straight shafts and large primary and small secondary cusps.

The geographic range of *G. neapeanensis* is restricted to a narrow region of the temperate coast of South Australia and Victoria. The other species are predominantly tropical. Iredale (1917a) reported, but did not describe, a species from Lord Howe Island that is well represented in the Australian Museum collections in Sydney. Occurrences elsewhere in the Indo-Pacific are primarily north of the Tropic of Capricorn in Mauritius, New Caledonia, the Marshall Islands and subsurface deposits at Eniwetok.

Specimens are typically recovered from washings of sublittoral algae along with specimens of *Tricolia*. They are easily confused with other minute 'pheasant shells' and must be examined microscopically to see the diagnostic shell and opercular features. The earliest fossil record of the subfamily is from the Pliocene of Jamaica. There are no reports of fossil specimens from Tertiary or Quaternary deposits in Australia.

Subfamily Tricoliinae

This subfamily is diagnosed by the presence of porphyrin shell pigments, which fluoresce under ultraviolet light and are not known in any other trochoideans. They are also the only trochoideans in which there is sexual dimorphism in the size of

the adult shell and animal, and in the size and number of teeth in the radula. Tricoliines lack the palatal sinus characteristic of the Gabrieloniinae and lack the parietal lamella characteristic of the Phasianellinae.

The genus *Tricolia* is represented by five species in Australia, which were reviewed by Robertson (1985a) under family Tricoliidae. Following Iredale (1924), Australian authors have treated these minute-shelled species under *Pellax*. However, the type species of *Pellax* is a member of the family Eatoniellidae (Ponder 1965a). Hickman & McLean (1990) provided a revised and illustrated characterisation of the subfamily.

The shell is small to minute (less than 10 mm high) and relatively sturdy, with an oblique aperture and a glossy surface with a variegated colour pattern (Fig. 15.59A). Pigmentation patterns are unusually variable, and different forms predominate in different geographic regions. As in the other two subfamilies of pheasant shells, Phasianellinae and Gabrieloninae, interior nacre is lacking. In instances of sexual dimorphism in shell size, the female attains the larger shell size. Smaller males are found on the shells of the females during the breeding season. The south-western Australian species, *Tricolia tomlini*, develops long branching periostracal hairs that are unique in the Trochoidea. The exterior calcified opercular pad is smooth in the Australian species and closely resembles that of the Phasianellinae, but there is an axial pit in the juvenile operculum that is lacking in phasianellines.

Features of the external anatomy are illustrated in Figure 15.59B. Although cephalic lappets are absent, the rest of the epipodium is more complex than in the primitive turbinid subfamilies. The three pairs of epipodial tentacles have basal sensory papillae, and the inhalant neck lobe is finely fringed. Sexual size dimorphism in the animals is not associated with any noticeable dimorphism in features of external anatomy.

The tricoliine radula is illustrated in Figure 15.59C, D. Sexual dimorphism is well documented in the radula of *Tricolia variabilis* (Robertson 1971a, 1985a) and is expressed not only as a difference in size and numbers of teeth, but also in tooth morphology. The radula is smaller in the male and contains half the number of marginal teeth per row, and the cusps on the rachidian and laterals differ in their shape. The typical ovate turbinid rachidian consisting of a cusplless basal plate is seen in most species of *Tricolia* (Fig. 15.59C), but in *Tricolia variabilis* and several other Australian species the rachidian has disappeared and the inner two lateral teeth are partially fused producing a single bilaterally symmetrical bicuspidate 'pseudocentral' in the rachidian position (Fig. 15.59D).

The anatomy of the Australian species has not been documented, but information on the type species, a well-known European species (see Robertson 1985a and references therein) indicates that it is not significantly different from that of other trochoideans.

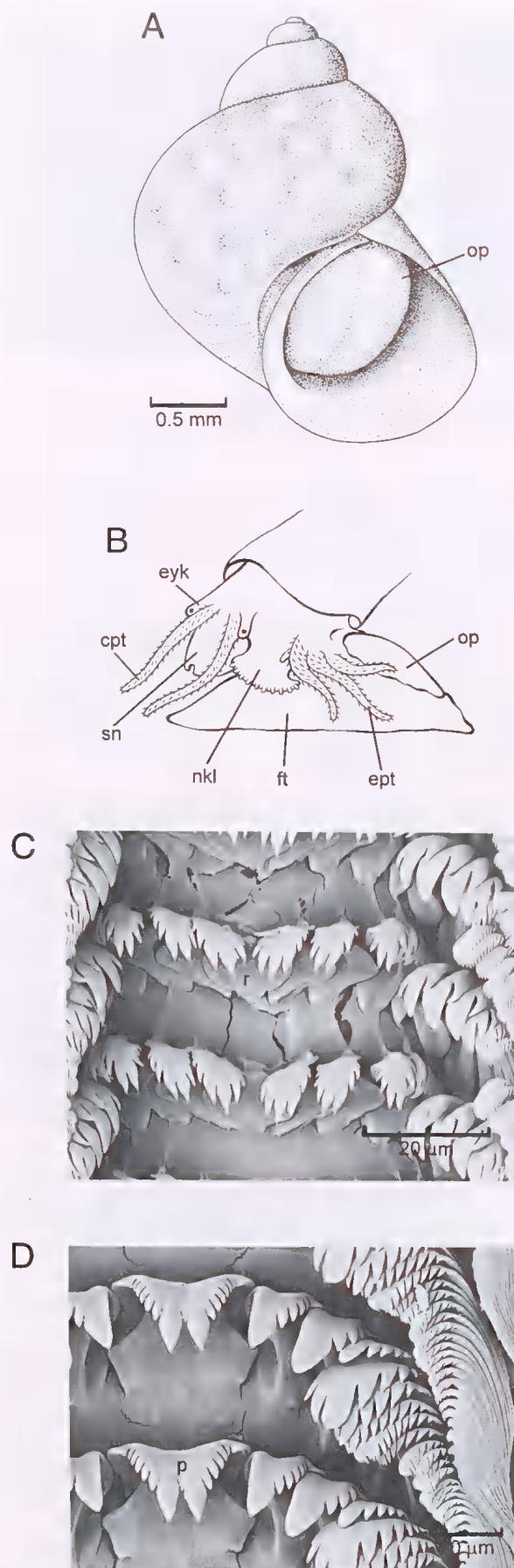


Figure 15.59 Family Turbinidae, subfamily Tricoliinae. A, B, *Tricolia variabilis*: A, shell with operculum, apertural view; B, external features of head-foot. C, D, portions of radulae: C, *Tricolia fordiana*, several transverse rows, showing the cusplless rachidian plate (r); D, *Tricolia variabilis*, from Norfolk Island, teeth on one side of radula; note the fused, bicuspidate pseudocentral tooth (p). cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; p, pseudocentral tooth; r, rachidian plate; sn, snout.

[A, S. Weidland; B, M.E. Taylor; C, D, G. Avern]

Tricoliines occur predominantly in shallow water (less than 6 m) on marine plants, including a great variety of red, brown and green algae and seagrasses. They are among the most abundant gastropods recovered from algal washings from many nearshore habitats. Gut contents indicate that they graze on surface films (C.S. Hickman personal observation). Pairing of males and females occurs during the breeding season, and *Tricolia variabilis* deposits its eggs in gelatinous benthic egg masses (Hickman 1992 and references therein). *Tricolia* specimens have been reported from the guts of a variety of fish predators (see Robertson 1985a). During some seasons and at some localities, shells of living animals may be heavily encrusted with coralline algae (C.S. Hickman personal observation).

Although, *Tricolia* has a predominantly tropical Indo-Pacific distribution, species occur around the entire Australian coastline. The three endemic Australian species (*T. gabiniana*, *T. rosea* and *T. tomlini*) are restricted to the southern Australian temperate region, extending into the eastern and western overlap zones. No species occur in New Zealand.

There is no published Tertiary fossil record for the group. However, specimens are abundant in some Pliocene and Quaternary beds, and two undescribed species occur in the Pliocene of Western Australia (C.S. Hickman personal observation).

Subfamily Phasianellinae

The third subfamily in the 'pheasant shell' group is diagnosed by the presence of a weak lamella that supports the operculum against the parietal region of the shell as the animal emerges or retracts. The surface of the shell is unique in the presence of fine spiral capillary lines that interrupt the wavy axial bands of pigment; and the radula lacks a functional rachidian tooth.

The genus *Phasianella*, the only genus in the subfamily, is based on the Australian species *Buccinum australis*. This name has a large number of synonyms owing to considerable local variation in shell form and colour pattern. Cotton (1959a) reviewed the Australian species and their forms, and Robertson (1958, 1985a) provided more detail on the morphological features of the subfamily and discussed its relationship to the other two pheasant shell subfamilies. The common name for these shells alludes to their bright colours and variegated patterns, which led earlier authors to treat them under a single family Phasianellidae. In Hickman's (1995) phylogenetic analysis, the three pheasant shell subfamilies (Gabrieloninae, Tricoliinae and Phasianellinae) form a distinct (unnamed) clade, but the relationships of the three taxa are unresolved.

The shells of *Phasianella* (Fig. 15.60A) are large relative to those of *Gabrielona* and *Tricolia*, but resemble them in lacking interior nacre and in the general appearance of the shell and operculum. The shell has a characteristic elongate profile, oval aperture and smooth glossy surface, as well as a brittle quality that results in a peculiar pattern of post-mortem breakage of empty shells. The ovate operculum, with its smooth, convex outer calcareous pad, is distinct from those of other turbinids. It most closely resembles the tricoliine operculum, which also has a convex exterior, but it never develops the radiating ridges found on some tricoliine opercula.

The external anatomy is illustrated in Figure 15.60B. The epipodium is more complex than in tricoliine species, with well-developed cephalic lappets and finely fringed inhalant and exhalant neck lobes that can be enrolled into semitubular siphons. The epipodial tentacles are long and slender. The anterior end of the highly extensible foot can be enrolled and used both to probe and to reach and grasp as the animal crawls on marine plants.

Major features of the phasianelline radula are illustrated in Figure 15.60C–E. The tooth shafts show a distinctive pattern of thickening and basal expansion (Fig. 15.60E). The central complex is highly modified (Fig. 15.60C, D). The rachidian tooth is lost and

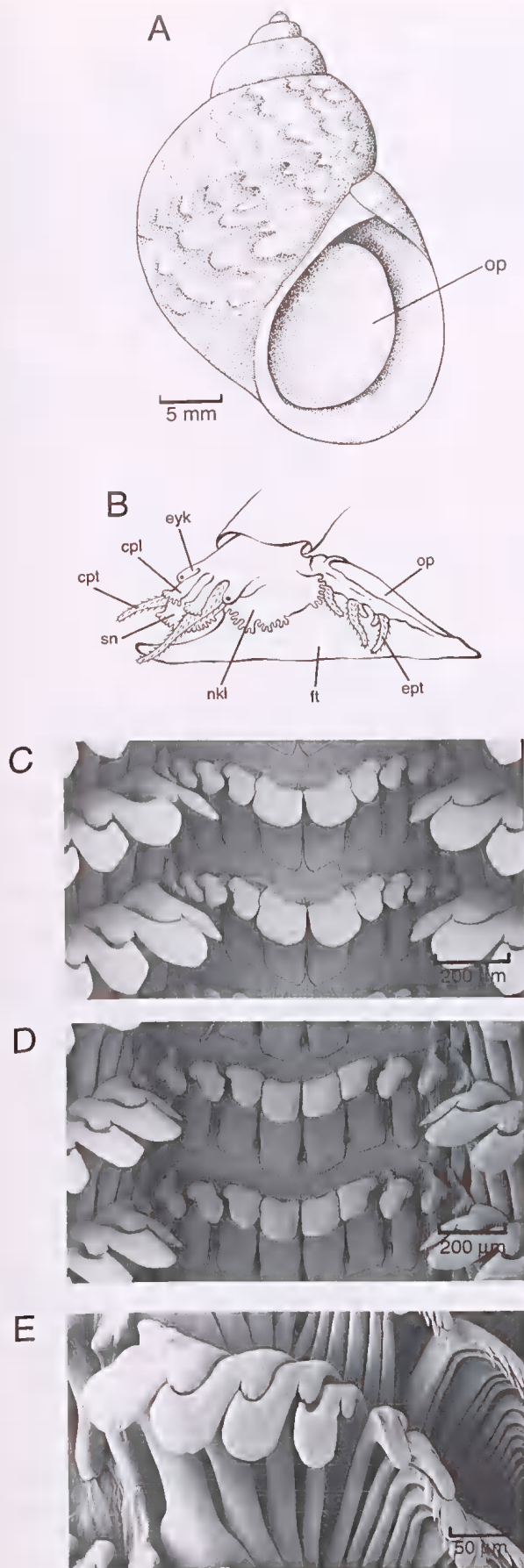


Figure 15.60 Family Turbinidae, subfamily Phasianellinae. **A**, *Phasianella ventricosa*, shell with operculum, apertural view. **B**, *Phasianella australis*, external features of head-foot. **C–E**, portions of radulae: **C**, *Phasianella ventricosa*, two transverse rows showing the lateral and inner marginal teeth, the rachidian tooth is lost; **D**, *Phasianella australis*, two transverse rows showing the lateral and inner marginal teeth, the rachidian tooth is lost; **E**, *Phasianella variegata*, from New Caledonia, showing details of the interlocking cusps of the four inner marginal teeth. **cpl**, cephalic lappet; **cpt**, cephalic tentacle; **ept**, epipodial tentacle; **eyk**, eye stalk; **ft**, foot; **nkl**, neck lobe; **op**, operculum; **sn**, snout.

[A, S. Weidland; B, M.E. Taylor; C–E, G. Avern]

the five lateral teeth have lost the mid-shaft bend. Shafts and bases are fused into single undifferentiated elements that are in turn fused to the radular membrane along their entire length. The cusps on the inner lateral teeth may be in contact, but they are never fused. Cusp size decreases from inner to outer laterals.

Animals are nocturnal and, although they may be relatively common in seagrass beds and on macroalgae, they are seldom seen during the day. Like other trochoideans that live on marine plants, they graze on epiphytic coatings rather than on plant tissue. They are preyed upon by octopuses, which apparently are able to remove the animal without boring or breaking the shells. Shell accumulations mark some octopus dens (Hickman unpublished data).

The genus *Phasianella* is predominantly temperate in its Australian distribution, and three of the four species (*P. australis*, *P. variegata* and *P. ventricosa*) are endemic to Australia. The genus level names *Orthomesus* and *Mimelenchus*, proposed for *P. variegata* and *P. ventricosa*, respectively, are considered to be junior synonyms of *Phasianella*.

Phasianella first appears in the Miocene of the Indian Ocean (Java and Australia). Although shells are not abundant in the Australian Neogene, there are horizons in the Pliocene in Western Australia that contain dense concentrations of opercula (C.S. Hickman personal observation). There is one named species that is extinct, *P. dennanti*.

Family Trochidae

The second of the two largest trochoidean families is diagnosed and distinguished from its sister family Turbinidae by a reduction in the length of the growing edge of the operculum and an inability to add calcium salts to the exterior surface of the operculum. The trochid rachidian tooth lacks the secondary flap or peg that provides additional attachment to the radular membrane, and the lateral teeth lack the distinctive mid-shaft bend that is characteristic of the turbinid radula (Hickman & McLean 1990). The rachidian tooth almost always has a distinct shaft and cusp, and the rachidian and laterals differ markedly in form in the two families.

In the most comprehensive treatment of Australian trochids, Cotton (1959a) classified genera and species under seven subfamilies: Calliostomatinae, Cantharidinae, Gibbulinae, Margaritinae, Monodontinae, Trochinae and Umboniinae. Hickman & McLean (1990), however, revised the family to include ten major subfamilies (Eucyclinae, Margaritinae, Trochinae, Stomatellinae, Calliostomatinae, Solariellinae, Halistylinae, Umboniinae, Tegulinae and Lirulariinae) and three minor subfamilies (Cataeginae, Trochaclidinae and Thysanodontinae), and this is the classification used here. For phylogenetic analysis of the relationships of trochid tribes and subfamilies, see Hickman (1995).

Two of the major subfamilies, the Tegulinae and Lirulariinae, are not represented in the Australian fauna, and only the other major subfamilies are treated herein. Of the seven subfamilies in Cotton's (1959a) treatment, only four (Margaritinae, Trochinae, Calliostomatinae and Umboniinae) were recognised at subfamily rank by Hickman & McLean (1990). These authors also reduced Cantharidinae and Gibbulinae to the rank of tribe (as Cantharidini and Gibbulini) under Trochinae, and synonymise Monodontini with Gibbulini. They also recognised four additional major subfamilies, each of which is prominent in the Australian fauna. The Eucyclinae and Solariellinae are distinctive subfamilies containing many taxa formerly treated under Margaritinae. The Stomatellinae, formerly treated as a distinct family, are recognised as a trochid subfamily. The Halistylinae are recognised as a subfamily in which a significant endemic Australian radiation has occurred.

Of the minor subfamilies, the Cataeginae have not been reported from Australia, and the Trochaclidinae are so poorly known anatomically and so poorly represented in the Australian fauna that they are not treated herein. Marshall (1995) has recognised two extinct and three extant trochaclidine species from Australia.

15. PROSOBRANCHS

However, the five species are represented collectively by a total of ten shells, and the Australian records, at present, appear to represent outliers of a distribution that is centred in New Zealand. Members of the third minor subfamily, the Thysanodontinae, occur primarily below 200 m off New Zealand, Australia and southern Africa. Although thysanodontines have an unusual radula (Marshall 1988a) the protoconch sculpture is typically calliostomatine. Accordingly, this group is treated under the Calliostomatinae.

There are 50 genus-level names in the Trochidae that are based on species endemic to the Australian fauna. Although many of these names are regarded as synonyms or applied primarily as subgenera, there are good arguments (suites of unique derived features) for validity of most of the names at the genus level (Hickman unpublished data). The number of available names is less an artefact of taxonomic 'splitting' than it is a reflection of elevated diversity of the family in Australasia. Systematic revision and understanding of the evolution of this large and important cosmopolitan family cannot be achieved without careful study of the Australian fauna. Although more than 400 species names have been used for trochids in the Australian fauna, some of them are junior synonyms of the most common and widespread species. There are many shells in museum collections for which there is no name at this time.

Trochid shells are highly variable in size, shape, thickness, ornamentation and pigmentation. The large top shells or trochus shells are among the most abundant, conspicuous and economically valuable molluscs in the tropical reef fauna. On rocky shores, the sturdy-shelled species of the distinctive temperate Australian genus, *Austrocochlea*, have assumed numerical dominance as grazers in intertidal mollusc communities. On marine plants, especially the seagrasses and the red and brown algae, the colourful shells of endemic genera and species of cantharidine trochids are a hallmark of the Australian molluscan fauna. Trochids have undergone a remarkable series of radiations into infaunal communities in Australia, typified by the high-spined, polymorphically pigmented necklace shells of the genus *Bankivia*, which live subtidally on high energy beaches and wash up by the millions during storms.

The external anatomy of the head-foot of trochids is more varied than that of turbinids. The foot and epipodium are relatively unspecialised in the primitive subfamilies, but there are elaborate innovations in the more highly derived subfamilies. The neck lobes are most subject to elaboration and have been modified to form complicated inhalant and exhalant siphons in the infaunal trochids. The anterior end of the foot in cantharidine trochids and some trochine lineages is modified for grasping marine plants and, in umboniine and solarielline trochids, for burrowing. A number of distinct grades of complexity are apparent in the form of trochid ctenidia. The primitive grade is bipectinate with a short afferent membrane, and the most highly derived grade is fully monopectinate.

The trochid radula lacks the uniform plan that unites the turbinid subfamilies, and each of the trochid subfamilies has its own distinctive radular plan. These plans were illustrated by Hickman & McLean (1990) and are represented in the subfamily treatments below.

The internal anatomy is as described for the superfamily and does not differ from that of turbinids. The anatomy is best known for European species of *Gibbula*, *Monodonta* and *Calliostoma* (Fretter & Graham 1962). Hickman (1992) reviewed the present knowledge of reproduction and development in the trochid subfamilies and tribes.

Trochids occur in most marine habitats and microhabitats, although none is adapted to live in the very highest portions of the intertidal zone or in fine-grained sediments (silt and mud). Although many trochids are routinely collected from under rocks (for example, species of *Canculus*, *Euchelus* and *Gena*), this habitat is only a daytime refuge for many nocturnal, negatively phototropic species. Washings from stones and marine algae are one of the richest sources of minute-shelled trochids (less than 5 mm high), which are as poorly studied in Australia as in other parts of the world.

There are approximately 50 described species of Australian Tertiary trochids, primarily from the basins of Victoria and South Australia. There are many more undescribed fossil taxa, especially in the faunas of the Perth Basin in Western Australia (C.S. Hickman personal observation). Unconsolidated sediments of late Pleistocene and Holocene age contain shell concentrations that are subject to mixing with the modern fauna, especially through the dredging of bays and harbours. It would be useful to pay greater attention to these deposits as a record of local extinctions associated with global climate change.

Subfamily Eucyclinae

This trochid subfamily is diagnosed by a suite of novel radular features that includes prominently 'hooded' rachidian and lateral teeth with shafts expanded basally into pegs and flanges that fit into deep pockets on adjacent teeth; well-developed, faceted, rectangular latero-marginal plates; and numerous, extremely fine marginal teeth, the outermost of which is expanded into a mitten-shaped element.

The eucycline genera and species have a long history of allocation to at least four different trochid subfamilies as well as to several families of extinct species that have been classified outside the Trochoidea. Cotton (1959a) treated the Australian genera and species under the trochid subfamily Margaritinae. The history of this group was discussed by Hickman & McLean (1990) who also enlarged and redefined the Eucyclinae to include three tribes, two of which are represented in the Australian fauna. The deep-water (> 200 m) tribe, Calliotropini is present, but not well documented, in the Australian fauna. Until recently there was a single named species, *Calliotropis glyptus*, endemic to the continental slope off New South Wales. Jansen (1994a) described four new endemic species (*C. echidna*, *C. carinata*, *C. canaliculata* and *C. lamellifera*) from the Queensland and New South Wales continental slopes. According to C.S. Hickman (personal observation) there are additional unnamed species from Victoria. The familiar shallow-water members of the tribe Chilodontini are better known, and the Australian fauna includes approximately 27 species in eight genera. Five of these species were described recently by Jansen (1994b). The most familiar species in this subfamily are those in the *Euchelus* group of genera. Photographs and scanning electron micrographs of the shells, animals and radulae of several Australian species were included in the study by Hickman & McLean (1990).

The shells of the common members of the *Euchelus* group typically are ovate, small (less than 10 mm high) and thick, with ornate radial and axial sculpture that produces characteristic beaded, scaly, or fine granular patterns (Fig. 15.61A). The aperture is nearly circular, interior nacre is conspicuous, and genera and species are most easily identified by characteristic patterns of columellar denticles, and denticulation or lirite thickenings of the outer lip. Colouration is typically an inconspicuous cream, fawn or brown, occasionally with red or pink blotches. The common beaded wide-mouth, *Granata imbricata*, is an aberrant member of this group having a depressed spire and greatly expanded final shell whorl (Fig. 15.61B). Although a small vestigial operculum is retained, the animal cannot retract into the shell. Members of the deep-water tribe have larger, more delicate shells (Fig. 15.61C) that are usually covered with a thin periostracum.

The basic features of eucycline external anatomy are illustrated in Figure 15.61D. The foot has a well-developed epipodium that is not strongly differentiated, although it is often finely divided into numerous epipodial tentacles of several ranks. The fine subdivisions of the neck lobes may have prominent dark pigment spots at their bases. Cephalic lappets also tend to have finely divided margins. The eyes are on short, stout eyestalks, and the cephalic tentacles are long, slender and densely covered with fine sensory micropapillae, as in other trochoideans.

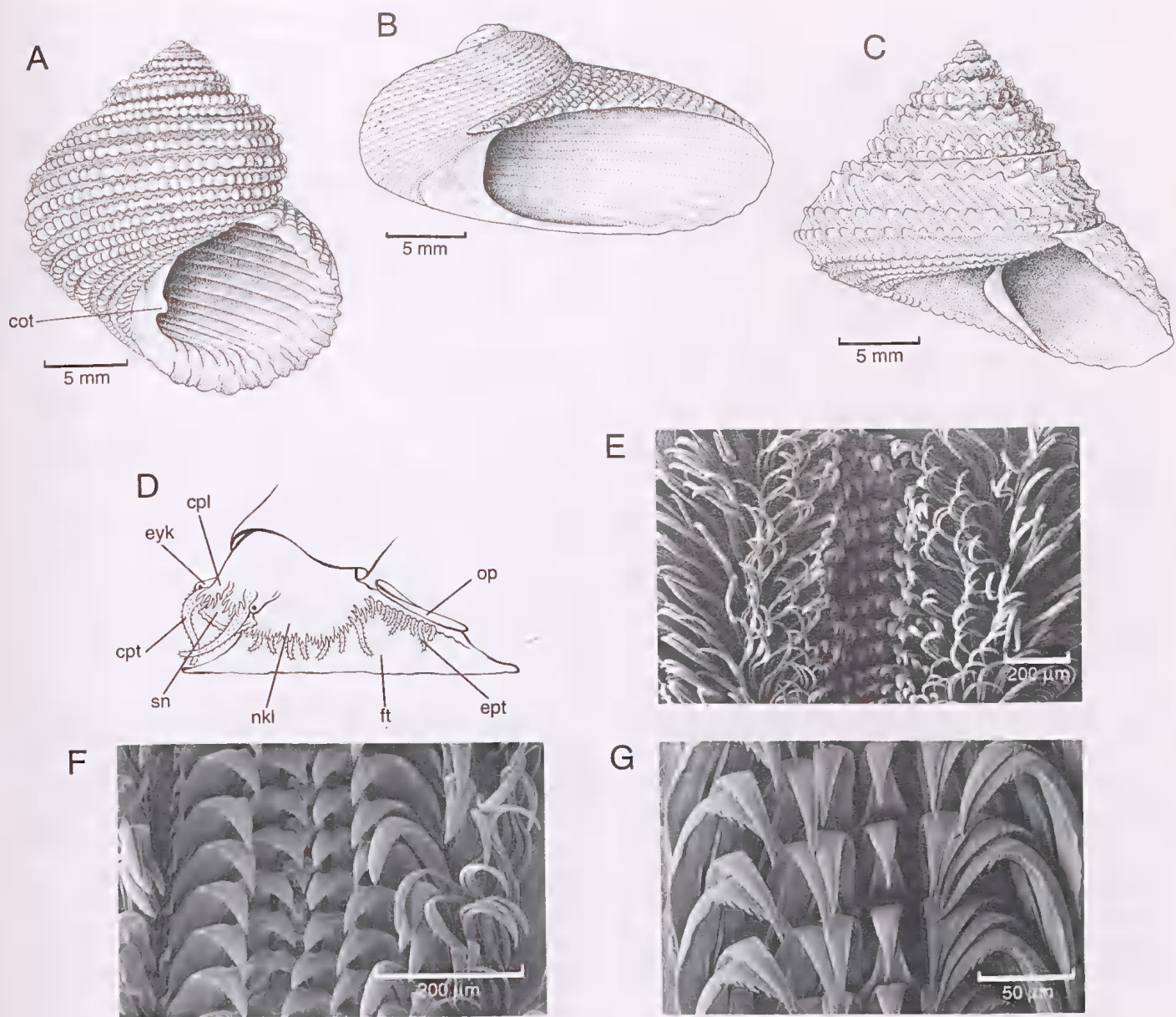


Figure 15.61 Family Trochidae, subfamily Eucyclinae. A–C, shells, apertural view: A, *Euchelus atratus*, showing columellar tooth; B, *Granata imbricata*, with expanded aperture; C, *Calliotropis glyptus*. D, *Euchelus atratus*, from the Philippines, external features of head-foot. E–G, mid-sections of radulae, showing teeth across several transverse rows: E, *Cidarina cidaris*, from the north-eastern Pacific; F, *Calliotropis glyptus*; G, *Granata imbricata*. cot, columellar tooth; cpl, cephalic lappet; cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; sn, snout. [A–C, S. Weidland; D, M.E. Taylor; E–G, C.S. Hickman]

The eucycline ctenidium is of the primitive trochid grade of organisation: it is bipectinate with a long free tip and correspondingly short dorsal afferent membrane, restricted to the region posterior to the transverse pallial vein.

The snout is short and terminates in a broad oral disc, which, in members of the deep-water Calliotropini, has prominent lateral expansions. Major features of the distinctive eucycline radula are illustrated in Figure 15.61E–G. It is most easily recognised by its unusually fine and numerous marginal teeth (Fig. 15.61E). The central tooth complex is narrow relative to the broad marginal tooth fields, and the number of lateral teeth in the deep-water subfamily is reduced from four to only three pairs, with cusps that are greatly enlarged relative to the rachidian (Fig. 15.61F). In the distinctive Australian genus, *Granata*, the rachidian and lateral teeth are equal in size, with unusually long overhanging cusps (Fig. 15.61G). The primary feeding action of this radula is inferred to be sweeping up of detrital particles by the marginal teeth. Selective deposit-feeding has been documented in the Calliotropini, and the animals have greatly enlarged hindguts that are packed with fine sediment (Hickman 1981b). Diets of the common shallow-water chilodontine species have not been

documented, but several of the Australian species are consistently associated with sponges. Thus, the possibility of sponge feeding should be investigated.

Members of the shallow-water tribe are restricted to hard substrata and rocky shores, whereas members of the deep-water tribe occur on fine soft sediments. The common intertidal and shallow subtidal species are negatively phototropic and their habits are poorly known because they spend daylight hours under rocks. Its enlarged foot provides *Granata imbricata* with strong powers of adhesion to rock surfaces, and when an individual is successfully pried from some of the sandstones of the Sydney area, cleavage of the rock leaves sandstone adhering to the foot. When animals are dislodged, they are unable to retract into the shell or to right themselves, although they actively twist and turn. When prodded, they emit copious amounts of a foul-smelling milky hypobranchial secretion of unknown composition, which is probably a predator deterrent (C.S. Hickman personal observation). One of the most familiar tropical species, *Euchelus atratus*, is often heavily encrusted with sponges. Several of the eucycline genera (for example, *Synaptocochlea*, *Hybochelus*, *Tallorbis*) have a predominantly tropical distribution in Australia

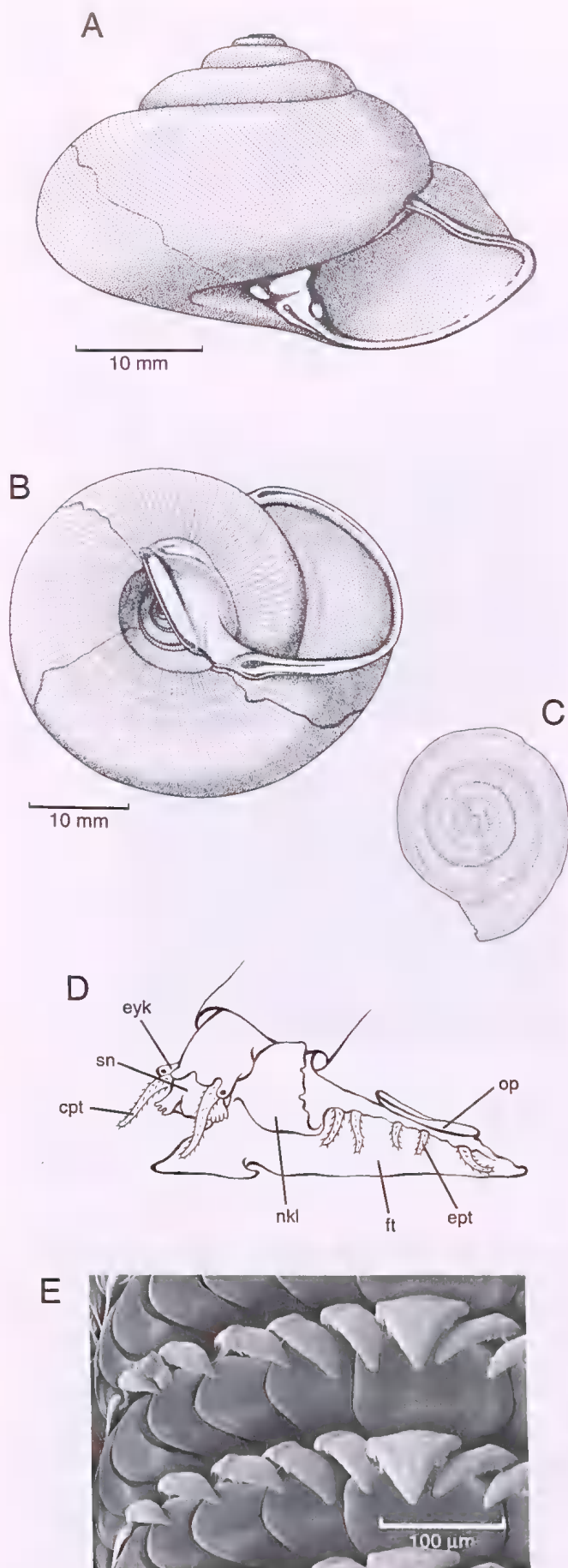


Figure 15.62 Family Trochidae, subfamily Margaritinae. *Gaza superba*, from Gulf of Mexico: A, shell, apertural view; B, shell, ventral view; C, operculum, outer surface; D, external features of head-foot; E, half of two transverse radular rows, showing details of the rachidian and lateral teeth. cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; sn, snout.

[A–C, C. Eadie; D, M.E. Taylor; E, C.S. Hickman]

and the species typically have a broader Indo-Pacific distribution. At the other extreme, *Granata* is monotypic and endemic to the southern half of the Australian coastline. The *Euchelus* complex of genera/subgenera is cosmopolitan and includes species that are widely distributed around the entire coastline as well as species that are more narrowly restricted to portions of the coastline.

Although the subfamily underwent an early evolutionary radiation in the Jurassic of Europe, it is only known in Australia from the Late Cretaceous. It is not a prominent element in Australian Tertiary faunas, and there are only two species that are relatively common in the Tertiary basins of Victoria and South Australia.

Subfamily Margaritinae

Members of this subfamily share many primitive features with the Eucyclinae, including the nearly circular aperture of the shell, the primitive ctenidium with a short afferent dorsal membrane and long free tip, and the relatively undifferentiated epipodium. The radula is distinctively modified, however, and the subfamily is easily distinguished and diagnosed by a large suite of radular features that includes greatly enlarged, broad, smooth, ovate, overlapping bases on the rachidian and lateral teeth. Shafts are reduced to a narrow region beneath each cusp, and cusps are long, overhanging and finely denticulate. The central tooth field is wide and there may be as many as nine pairs of lateral teeth. The marginal tooth fields are correspondingly reduced in width.

The Australian genera and species that Cotton (1959a) classified in this subfamily were either re-allocated to Seguenziidae or re-assigned to the trochid subfamilies Eucyclinae or Solariellinae by Hickman & McLean (1990). The reconstituted subfamily Margaritinae, based on radular features, includes a shallow-water group that is restricted to high latitudes, predominantly in the Northern Hemisphere, and a deep-water group that is cosmopolitan. The shallow-water tribe Margaritini is not represented in the Australian fauna, and the deep-water tribe Gazini of Hickman & McLean (1990), is represented by a single, as yet undescribed, bathyal species that occurs off the New South Wales coast (Hickman unpublished data). Marshall (1993) described a third margaritine tribe, Kaiparathini, a distinctive group of small-shelled species (generally less than 5 mm high) of the genus *Kaiparathina*, concentrated in a region of the western Pacific from New Zealand northwards along the Norfolk Ridge and Lord Howe Rise to New Caledonia and the Loyalty Islands. There are five living species and three extinct species, the oldest of which is Palaeocene. Australia is separated from this region in which these species occur by the Tasman Abyssal Plain and has no comparable oceanographic setting; there are no reported Australian occurrences of the group.

The shells of members of the deep-water tribe (Fig. 15.62A, B) have several distinctive features. The outer lip is thickened and reflected, which is an unusual feature in trochoideans, and the thin, smooth shell has an unusual opalescent sheen. An umbilicus is present, but it may be completely sealed off by a thin, translucent callus. The operculum is illustrated in Figure 15.62C.

Features of animals in the deep-water tribe are illustrated in Figure 15.62D. The anterior end of the foot has modified anchor-like lateral tips. The epipodium is relatively simple, with five pairs of epipodial tentacles and inhalant and exhalant neck lobes with entire margins. The eyes are on short, stout eyestalks and cephalic tentacles are slender, well developed and covered with fine sensory micropapillae as in other trochoideans. The ctenidium is of the same primitive grade of organisation as in the Eucyclinae, with a short afferent dorsal membrane and long free tip.

The snout is highly modified, with terminal lateral expansions that project as short tentacles. The snout modification is probably associated with deposit-feeding. The hindgut is enlarged and typically filled with fine sediment.

Features of the radula are illustrated in Figure 15.62E. The number of lateral teeth is highly variable in this subfamily; in the tribe Gazini there may be seven or more lateral teeth with strongly overlapping bases. There are eight laterals in the Australian species, and in the position normally occupied by the latero-marginal plate there are two inner marginal teeth that lack cusps and have irregular expanded bases. The marginal teeth have unusually long, finely denticulate shafts and the outer marginal cusps are fused.

Specimens of the undescribed Australian species are all from bathyal depths (below 299 m) on fine mud substrata off the coast of New South Wales. The numbers of specimens taken suggests that it may be relatively common. The stratigraphic range of the subfamily is from Upper Eocene to Holocene, although no members of either margaritine tribe are known from the Australian fossil record.

Subfamily Trochinae

The Trochinae are the largest of the trochid subfamilies in respect to numbers of genera and species and also the best-represented subfamily in Australia (see Pls 23.5, 23.6). The shells are extremely diverse in size, shape, apertural features and ornamentation, although there are genera and groups of genera that are easily recognised on the basis of shared shell features. Members of the Trochinae differ from the more primitive trochid subfamilies Eucyclinae and Margaritinae in the development of a relatively long dorsal afferent membrane connecting the ctenidial axis to the mantle skirt. They share a distinctive suite of radular characters that includes a notch in the top of the rachidian cusp; five pairs of lateral teeth of similar shape and gradually increasing in size; a unique, heavy, fused shaft and base on the first marginal tooth; and a prominent food-collecting groove beneath the cusps of the marginal teeth. Common names applied to Australian trochines include top shells, trochus shells, periwinkles and kelp shells.

Cotton (1959a) and other Australian authors have classified the species in this subfamily under four different subfamilies: Trochinae, Monodontinae, Gibbulinae and Cantharidinae. On the basis of radular and ctenidial characters, Hickman & McLean (1990) recognised a single subfamily with three tribes: Trochini, Gibbulini, and Cantharidini. There is no basis for distinguishing the Monodontini from the Gibbulini. The presence of a columellar denticle, which has been used to identify members of the Monodontini, cuts across clades in which a denticle may be present or absent; denticles when present are not all homologous. Some of the genera and subgenera are poorly defined and major revisions are needed for the species that have been classified under *Clanculus* and its subgenera, the *Monodonta*-like species that have been assigned alternatively to *Austrocochlea* and *Fractarmilla*, and species that have been moved about within the cantharidine group of genera and subgenera.

Variation in shell form in the subfamily is illustrated in Figure 15.63A–F. Shells range from minute (less than 4 mm) in the genus *Alcyna* (Fig. 15.63A) to the largest in the family (130 mm high) in the genus *Trochus* (Fig. 15.63B). They vary in shape, although the typical shape implicit in the term ‘trochiform’ is conical with a straight-sided spire and sharply demarcated flat base (Fig. 15.63B). Shells are usually thick and robust, with surfaces that range from smooth in some of the cantharidine species (Fig. 15.63C) to coarsely nodular (Fig. 15.63D). The aperture is oblique and strongly inclined to the axis of coiling in taxa such as *Tectus* in which the base is flat. The strength of columellar denticles varies from strong (Fig. 15.63D, E) to weak (Fig. 15.63F). Pigmentation patterns vary from solid colours to complex discordant patterns of stripes and zigzags (Fig. 15.63B, F). The nacreous layer is unusually thick in some of the species of commercial value.

The major features of the trochine head-foot are illustrated in Figure 15.63G. The elongate trochine foot is able to assume a range of shapes during locomotion and righting, and in lineages that live on marine plants the foot can be enrolled longitudinally

to grip blades or stipes. The epipodium is well developed, and the epipodial tentacles have prominent basal sensory papillae. Cephalic lappets and neck lobes are well developed and frequently have digitate margins. Both the epipodium and the foot tend to be conspicuously pigmented, with colours and patterning ranging from solid black to variegated patterns of red, grey, yellow and cream.

The snout is relatively broad and terminates in a well-developed oral disc that is split mid-ventrally in many members of the tribe Gibbulini. The major features of the trochine radula are illustrated in Figure 15.63H–K. The central and marginal tooth fields are both well developed and form arcuate rows in which tooth bases and cusps coincide. The rachidian is flanked by five pairs of lateral teeth with overhanging cusps of similar shape and size that are either similar (Fig. 15.63H) or gradually increase in size from inner to outer laterals (Fig. 15.63I, J). The rachidian tooth and the lateral teeth have a base that is broadly expanded, as in the Margaritinae, but which narrows towards the cusp to form a definite shaft. The rachidian cusp is sometimes reduced in size, but is never lost. A poorly developed hood is present, but it never assumes the prominence of the eucycline hood. Marginal teeth are steeply graded in size and shape: inner marginals have robust shafts and prominent overhanging cusps, and outer marginals have fine shafts with a range of patterns of subdivision of the cusps (Fig. 15.63K). The innermost marginal tooth cusp is attached to a fused and enlarged shaft and base. Gut contents and feeding tracts in many species indicate a predominant mode of feeding on surface films.

Members of this subfamily are prominent elements in many intertidal and shallow subtidal communities around the entire Australian coastline. Eighteen generic names in this subfamily are based on species endemic to Australia. The diversity and abundance of trochine species is highest on the temperate southern half of the coastline on firm substrata including rock, seagrass blades and red and brown algae. Many of the more northern, tropical taxa (for example, *Trochus*, *Chrysostoma*, *Monodonta*) are broadly distributed in the Indo-Pacific, whereas many of the temperate taxa (for example, *Austrocochlea*, *Cantharidella*, *Phasianotrochus*) are more narrowly restricted to the southern portion of Australia, with some ranges that extend to New Zealand. The endemic *Austrocochlea* complex of species contains some of the most familiar and abundant rocky intertidal gastropods on temperate Australian shores. Variation in shell-banding patterns was studied by Underwood & Creese (1976), and Parsons & Ward (1994) used genetic data to argue that *A. constricta* is, in fact, a complex of three discrete species.

The trochus shell industry in Australia is based on the large-shelled (125 mm) tropical Indo-Pacific species *Trochus niloticus* (the ‘button shell’); see also Chapter 1. The early history of the industry in Queensland and Western Australia (which also included smoked meat) was reviewed by Allan (1950). The industry is controlled by permit through State fisheries departments, and poaching is a major problem. Cantharidine species were used in jewellery by Aborigines prior to western colonisation of the continent. *Phasianotrochus eximius* was at one time used for knobs for ladies’ hat pins, and *P. irisodontes* has been harvested commercially in Tasmania for the manufacture of necklaces for the tourist industry. Shells were treated to expose the nacreous layer and strung whole, sometimes after staining with aniline dyes. Collection and treatment of shells for ‘Hobart necklaces’ were described by Mawle (1918).

All three tribes are of Mesozoic origin, the Trochini appearing first in the Middle Triassic. There are seventeen extinct named species from Tertiary and Quaternary beds in Australia in addition to fossil shells that have been assigned to six extant species; two taxa have been compared with extant species. The number of unnamed small-shelled species in museum collections is potentially large, and the range of variation within and between stratigraphic horizons is sufficiently large that the number of new names required cannot be determined without additional study (C.S. Hickman personal observation).

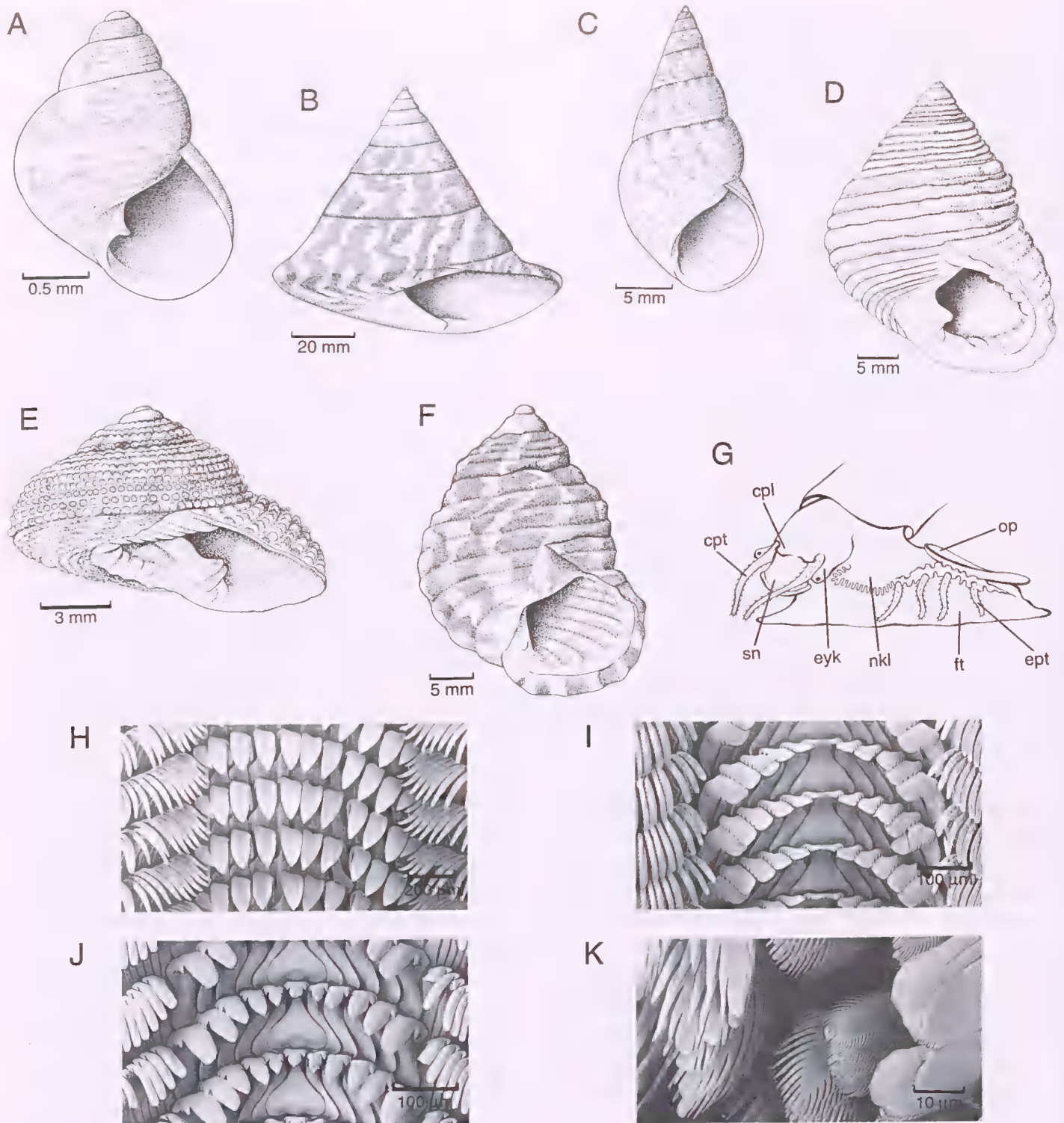


Figure 15.63 Family Trochidae, subfamily Trochinae. A–F, shells, apertural view: A, *Alycyna* sp.; B, *Trochus niloticus*; C, *Phasianotrochus eximius*; D, *Monodonta labio*; E, *Clanculus* (*Euryclanculus*) *floridus*; F, *Austrocochlea constricta*. G, *Monodonta labio*, from Japan, external features of head-foot. H–J, several transverse radular rows, showing the curve of the rows and the rachidian, lateral and inner marginal teeth: H, *Tectus pyramis*, from Hong Kong; I, *Austrocochlea constricta*; J, *Thalotia conica*; K, *Trochus intextus*, from Hawaii, cusps of the outer marginal teeth. cpl, cephalic lappet; cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; sn, snout. [A–F, S. Weidland; G, M.E. Taylor; H–J, G. Avern; K, C.S. Hickman]

Subfamily Stomatellinae

The so-called wide-mouths, cap ears or false ears of the subfamily Stomatellinae are the most highly modified trochids in shell form and external anatomy, and traditionally have been treated as a distinct family (for example, Cotton 1959a). However, the radula is barely distinguishable from those of the subfamily Trochinae. Hickman & McLean (1990) have provided a redefinition of the subfamily and reviewed the problems of historical treatment and confusion in nomenclature. Note that the family-level name Stomatellidae has priority over the name Stomatiidae, which has been used by some Australian authors (for example, Cotton 1959a; Iredale & McMichael 1962).

The Stomatellinae are the only trochoidean subfamily in which the opercula are completely lost. The animal is unable to retract into the flattened shell, and the enlarged metapodium is commonly autotomised when animals are disturbed. The ability to shed and regenerate the metapodium distinguishes members of this group from all other secondarily flattened trochoideans. In the phylogenetic analysis of Hickman (1995), Stomatellinae is the well-supported sister group of Trochinae.

Hickman & McLean (1990) tentatively recognised only five genera in the subfamily. All five (*Microtis*, *Pseudostomatella*, *Stomatia*, *Stomatella* and *Gena*) are represented in the Australian fauna. Although none is endemic to Australia, genus and species

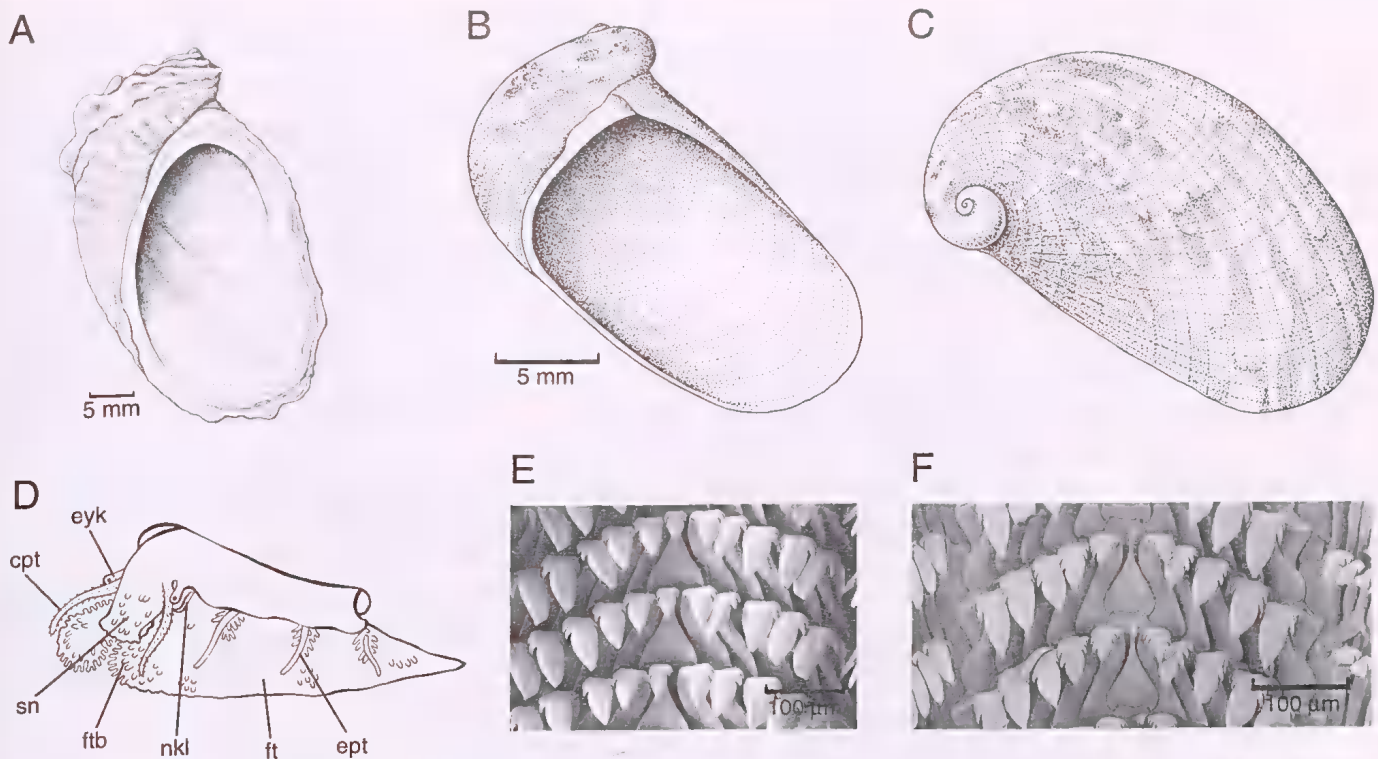


Figure 15.64 Family Trochidae, subfamily Stomatellinae. A, *Stomatia phymotis*, shell, apertural view. B, C, *Stomatella auricula*, shell: B, apertural view; C, abapertural view. D, *Microtis heckeliana*, external features of head-foot; note absence of operculum. E, F, portions of radulae showing central fields of several transverse rows: E, *Stomatella auricula*, rachidian and lateral teeth shown; F, *Microtis* sp., rachidian, lateral and inner marginal teeth shown. cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; ftb, foot tubercles; nkl, neck lobe (left); sn, snout. [A–C, S. Weidland; D, M.E. Taylor; E, C.S. Hickman; F, G. Avern]

diversity of the subfamily are centred in the Indo-West Pacific (C.S. Hickman personal observation). More than 30 specific names have been applied to species in the Australian fauna. Stomatelline species are highly variable in shell form and colour patterns, and a review of the group is needed.

The shells (Fig. 15.64A–C) typically have few whorls, a widely expanded aperture and brilliant polychromatic interior nacre. Apertural denticles and elaborations are lacking. The shell exterior ranges from coarsely sculptured and carinate in *Stomatia* (Fig. 15.64A) to highly polished or microscopically striate in *Stomatella* and *Gena* (Fig. 15.64B, C). Colour patterns frequently are polymorphic within local species populations, and include solid black or bluish-black and various mottled or flammulated varieties of intermixed black, white, cream, yellow, reddish brown and pink. In apertural view (Fig. 15.64A, B), the colour pattern ends before it reaches the long, arcuate columellar lip.

The major features of stomatelline external anatomy are illustrated in Figure 15.64D. In addition to the enlargement of the metapodium, which forms a pouch that partially encloses the posterior margin of the shell, the stomatelline foot is unique in the elaboration of the exposed dorsal surface into numerous, closely spaced, small, simple tubercles as well as larger branched tubercles. The posterior epipodium is relatively poorly developed: it is not distinctly demarcated on the foot, and there are never more than three epipodial tentacles. The anterior portion of the epipodium is better developed in some species, and may include branched cephalic lappets and well-developed inhalant and exhalant neck lobes that are partially enrolled to form prominent troughs directing currents through the mantle cavity. The eyestalks are short and thick relative to the very long and slender cephalic tentacles.

The bipectinate left ctenidium is similar to that in the Trochinae, sharing the derived condition of a long dorsal afferent membrane.

The snout is short, with a broad terminal oral disc that is not split mid-ventrally. The major features of the stomatelline radula are illustrated in Figure 15.64E, F. The only feature that clearly distinguishes the stomatelline radula from that of the Trochinae is a dramatic reduction in many species in the size of the entire

rachidian tooth and especially its cusp. The inner marginal tooth has the same characteristically thickened base and shaft that serves as a pseudo-latero-marginal plate in both subfamilies. Diets are undocumented.

The subfamily is predominantly tropical and subtropical in its distribution, although it is represented at temperate latitudes in Australia. In contrast to the Trochinae, there is no generic endemism in Australia. Animals may be collected primarily from beneath rocks at intertidal and shallow subtidal depths. The photonegative animals of *Stomatella auricula* often cluster under a single rock and respond to exposure by crawling rapidly away from the light back to the lower surface of the rock. If disturbance is sudden, they drop off into the water column and autotomise the metapodium, falling to the bottom in two pieces.

The fossil record of the Stomatellinae cannot be traced with certainty to rocks older than Pliocene age. A single extinct species, *Gena incola*, has been described from the Pliocene of South Australia; stomatelline shells are never abundant in the fossil record (C.S. Hickman personal observation).

To prevent autotomy of the metapodium, it is necessary to relax animals carefully in magnesium chloride prior to fixation.

Subfamily Calliostomatinae

The calliostomatine group of trochids is clearly diagnosed by a suite of derived radular characters that includes a delicate rachidian tooth with a long finely serrate cusp and finely serrate lateral cusps of similar size and shape; the differentiation of marginal teeth into many distinct cusp morphologies; and the enlargement of the innermost marginal tooth into a heavy hooked element. Members of the subfamily also share a unique honey-comb pattern on the protoconch, projecting papillae on the oral disc, a prominent pseudoproboscis and a cuticularised lining of the buccal cavity.

The subfamily and historical treatment are reviewed by Hickman & McLean (1990). The Calliostomatidae are sometimes treated as a separate trochoidean family (Finlay 1927a; Golikov & Starobogatov 1975). Whereas some authors have recognised a single calliostomatine genus, *Calliostoma*, and a series of

15. PROSOBRANCHS

subgenera (Clench & Turner 1960), Cotton (1959a) used 12 names of generic rank for species in the Australian fauna. There is greater diversity in shell form in the austral calliostomatine species than elsewhere in the world, although there are no comparative data on anatomical diversity. Anatomy of the European *Calliostoma zizyphinum* was discussed and figured by Fretter & Graham (1962), and Crofts (1955) classic work on larval development, muscle morphogenesis and torsion in primitive gastropods is partially based on this species. A modern review of this subfamily in Australia, incorporating comparative anatomical data, is needed.

Calliostomatine shells are illustrated in Figure 15.65A–C and *Calliostoma armillatum* is illustrated in Plate 23.4. Shells are small to medium-sized and are frequently referred to as 'top-shaped'. The obliquely inclined aperture has a characteristic angulation where the columella meets the lower lip. The majority of species do not have an open umbilicus. The spire is frequently straight sided (Fig. 15.65A, B), although it may have rounded whorls or rapidly expanding whorls that produce a concave upper spire profile, as in the endemic New Zealand genus *Maurea*. There is usually a sharp peripheral demarcation, often with a thickened spiral rib, between the spire and the base of the shell (Fig. 15.65B). The monotypic Australian genus, *Sinutor*, is unique in its sinistral shell coiling (Fig. 15.65C). Spiral ribs, plain or with nodules, are the predominant form of sculpture. Pigmentation is variable. The orange and violet pigments produced by several species are uncommon in other subfamilies. Regularly spaced blotches of pigment are common on the peripheral keel (Fig. 15.65B).

The main features of calliostomatine external anatomy are shown in Figure 15.65D. The foot is rounded anteriorly and tapers to a point posteriorly. It is typically papillate and often brightly pigmented. The neck lobes have margins that are simple or scalloped. There are four or five epipodial tentacles with basal sheaths and sensory papillae that are more prominent than in most trochoideans. Cephalic tentacles are long and slender and cephalic lappets are relatively small or absent. The bipectinate left ctenidium with a long dorsal afferent membrane is a derived condition shared the Trochinae and Stomatellinae.

Many features associated with feeding are highly specialised. In addition to the papillate oral disc, pseudoprobooscis, and cuticularised buccal cavity lining, there are especially well-developed jaws. The calliostomatine radular plan is illustrated in Figure 15.65E, F. The rachidian and lateral teeth are reduced relative to the marginals (Fig. 15.65E). The long feathery cusps attach directly to broad, thin, overlapping basal plates. The considerable overlap between tooth rows is illustrated in the rachidian base, which is overlapped by the long curved triangular cusp (Fig. 15.65F). The robust, strongly cuspidate, innermost marginal teeth are the most prominent teeth in the radula. The inner marginals have heavy, flattened shafts. Some species feed on cnidarian polyps, although gut contents of other species suggest a broader range of food items, including sponges and tunicates. Calliostomatine carnivory and stereotyped behaviour toward prey species are documented by Perron (1975) and Perron & Turner (1978).

The subfamily has a cosmopolitan geographic distribution and a bathymetric range from the intertidal to the bathyal zones. The intertidal and shallow subtidal species occur on a variety of substrata, and many are characteristically associated with their preferred sessile invertebrate prey. *Calliostoma sensu stricto* does not occur in the Australian fauna. Among the genus-level taxa that occur in Australia, the subgenus *Salsipotens* is cosmopolitan, whereas other subgenera *Coralastele*, *Benthastelena*, *Fautor*, *Laetifautor* and *Sinutor* are all endemic to Australia. The distinctive New Zealand genus *Maurea* further illustrates the degree of generic-level endemism in this subfamily in the Oriental/Australasian region. There are a number of undescribed small- to minute-shelled Australian calliostomatine species (less than 5 mm) in museum collections (C.S. Hickman personal observation).

The earliest indisputable fossil occurrences are in Upper Cretaceous rocks, although there are Triassic and Jurassic shells that have a number of calliostomatine features. Two extant species and eighteen extinct named species, described under six generic names, occur in Australian Tertiary faunas, and shells are relatively common and well preserved (C.S. Hickman personal observation).

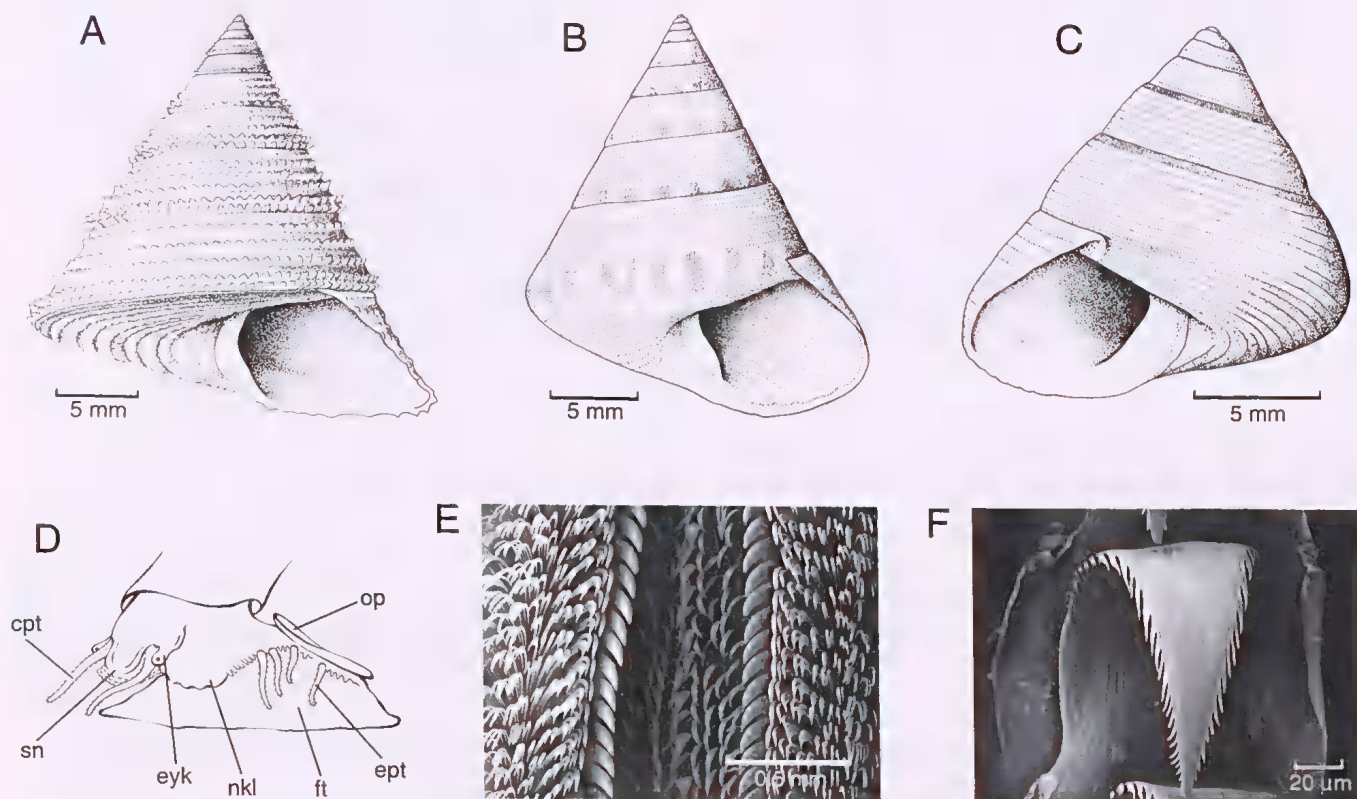


Figure 15.65 Family Trochidae, subfamily Calliostomatinae. A–C, shells, apertural view: A, *Calliostoma (Astele)* sp.; B, *Calliostoma monile*; C, *Sinutor incertum*, note sinistral coiling. D, *Calliostoma ligatum*, from the north-eastern Pacific, external features of head-foot. E, F, portions of radulae: E, *Calliostoma canaliculatum*, from the north-eastern Pacific, a few transverse rows showing most of the teeth; F, *Maurea benthicola*, from New Zealand, rachidian tooth. cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; nkl, neck lobe; op, operculum; sn, snout. [A–C, S. Weidland; D, M.E. Taylor; E, C.S. Hickman; F, G. Avern]

The small subfamily Thysanodontinae, proposed by Marshall (1988a) for a group of relatively small-shelled taxa (less than 10 mm high) is treated here since the group shares some features with calliostomatines. Thysanodontines have a suite of highly derived modifications of the anterior alimentary tract, including a long filamentous radular tooth with barbed tips. The protoconch, however, shares the distinctive calliostomatine hexagonal honeycomb pattern of protoconch ornamentation. Members of this small subfamily occur primarily below 200 m off New Zealand, Australia and southern Africa.

Subfamily Solariellinae

This specialised trochid subfamily is most readily diagnosed by a set of radular features that includes the reduction of the number of tooth rows to fewer than 30 and reduction of the number of marginal teeth to approximately ten per half row. There is a dip at the midline of each cusp row and pronounced differences in the sizes and shapes of lateral teeth. The oral surface of the snout is expanded laterally and covered with prominent tentaculate papillae, and the anterior end of the foot has well-developed lateral processes. Because of their offshore occurrence, solarielline species are not as well known as most other Australian trochids.

Hickman & McLean (1990) recognised ten solarielline genera with extant species; three are represented by named species in the Australian fauna. *Archiminolia* and *Minolops* are endemic to Australia and *Spectamen* is more broadly distributed at higher latitudes in the Southern Hemisphere. Marshall (1979) described three new species of *Microgaza* from the Kermadec Ridge, and there is at least one undescribed species, recognised by its distinctive smooth glossy shell, in the Australian fauna (C.S. Hickman personal observation). There are no shells in the Australian fauna comparable to the Oligocene–Recent taxa that have been described in the endemic New Zealand genus, *Zetela*. It is not always possible to distinguish members of the subfamily from the shell alone, and the Australian taxa were split for many years between Margaritinae and Umboniinae (see for example, Cotton 1959a). Hickman & McLean (1990) have reviewed the subfamily. The only recent species-level treatment is Herbert's (1987b) monograph of 32 species in the fauna of southern Africa.

A typical solarielline shell is illustrated in Figure 15.66A. Shells are small, usually less than 10 mm high, with whorl profiles that range from strongly biangulate to rounded. The aperture is circular and not strongly inclined to the axis of coiling, and an umbilicus is present. A beaded spiral cord sets off the umbilicus in many species, and there are often fine axial striation patterns within the umbilicus. Most shells are either smooth or have a predominance of coarse to very fine spiral sculpture. Shell surfaces range from dull to highly glossy and from unpigmented to pigmented with irregular blotches or discordant zigzag patterns. Shells may be so strongly convergent with those of margaritine or umboniine species that examination of the animal or radula is required in order to classify them.

The major features of solarielline external anatomy are illustrated in Figure 15.66B. Unlike the shell, the animal is easily recognised by striking modifications of the head region. In addition to the tentacular fringe on the edge of the oral disc and the lateral expansions of the anterior end of the foot, the cephalic tentacles are unusually long and slender (although this is not usually discernible in preserved animals) and the eyestalks and eyes are reduced in size. Cephalic lappets are absent. There are three or four pairs of epipodial tentacles and the neck lobes are reduced in size and complexity. The modifications of the oral disc and foot are related to habitat: animals have developed the ability to live on and burrow into sandy substrata and to extract food particles selectively from sediments. Animals also have a posterior elaboration of extensible metapodial tissue that is used in swimming, a foot-thrashing escape response shared by members of the Solariellinae (Herbert 1987b) and Umboniinae (Hickman 1983). The bipectinate left ctenidium shows the derived condition of a long dorsal afferent membrane common to the Trochinae, Stomatellinae and Calliostomatinae.

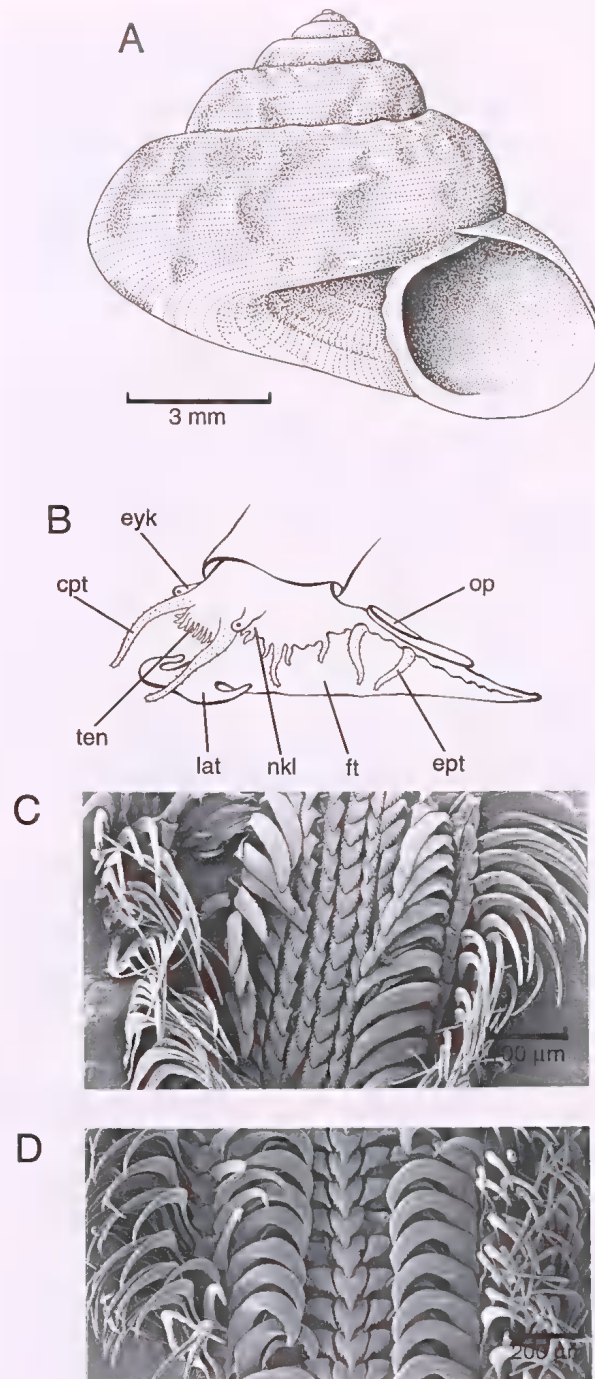


Figure 15.66 Family Trochidae, subfamily Solariellinae. A, *Spectamen philippense*, shell, apertural view. B, *Solariella peramabilis*, external features of head-foot. C, D, portions of radulae, showing all tooth types across a number of transverse rows: C, *Spectamen philippense*; D, *Solariella nuda*, from the north-eastern Pacific. cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; lat, lateral extensions of foot; nkl, neck lobe; op, operculum; ten, tentacular fringe of oral disc.

[A, S. Weidland; B, M.E. Taylor; C, G. Avern; D, C.S. Hickman]

The major features of the solarielline radula are illustrated in Figure 15.66C, D. This group has one of the most highly modified and easily recognised trochoidean radular plans. Herbert (1987b) and Hickman & McLean (1990) provided scanning electron micrographs showing radular features and discuss the functional significance of the radular features. Radular abnormalities are especially common in some populations. Gut contents contain a variety of organic constituents from the sediment, including annelid setae and fragments of crustaceans. There are few accounts of live animals. The Australian *Spectamen philippense*, the type of the genus, burrows rapidly and efficiently when it is not crawling on the sediment surface, where it makes stereotyped feeding movements in which the snout tentacles repeatedly rake down and through the sediment (C.S. Hickman personal observation).

15. PROSOBRANCHS

The subfamily has a predominantly extra-tropical, offshore distribution in cold water and a consistent association with unconsolidated sediments. It is absent from coral reefs. At lower latitudes it is restricted to deep water. The largest populations of dredged animals from the east coast of Australia are from embayments (Port Jackson, Jervis Bay, Twofold Bay), but offshore sampling on the open coast is insufficient to determine whether this is a real pattern. This is one of several trochoidean subfamilies in which brooding has evolved (Hickman 1992), but it is the only one in which brooding has been reported to take place in the mantle cavity (Herbert 1987b).

The fossil record of the subfamily begins in Cretaceous rocks. There are at least five extinct species in the Australian Tertiary (C.S. Hickman personal observation). Four of them are named. Specimens are not abundant but they are extremely well preserved and unequivocally solarielline. There are several possible occurrences in the Australian Cretaceous but material is not well enough preserved for clear assignment (C.S. Hickman personal observation).

Subfamily Halistylinae

The Halistylinae are a relatively minor subfamily of minute (less than 5 mm high), solid-shelled species diagnosed by a monopectinate ctenidium that lacks a free tip and has uniquely enlarged ctenidial sensory bursicles. Halistylines are unique among trochoideans in having eyes on the dorsal surface of the eye stalks. The operculum has a distinctive upturned fringe along the margin of each volution.

There are only three genera in the family. *Halistylus* is restricted to the Americas, predominantly North America, and *Botelloides* and *Charisma* are circum-Australian. Ponder (1985b) monographed the genus *Botelloides*. He noted the trochoidean identity of the genus (Ponder 1985a, 1985b), recognising similarities in the rhipidoglossate radulae of *Botelloides*,

Charisma and *Halistylus*. Iredale (1924) had observed that the species now allocated to *Botelloides* are distinct from the rissoid genera to which they had been assigned initially, but he did not suspect that they might be trochoidean. Although *Charisma* has been recognised as trochoidean, it has been treated under Liotiidae (Cotton 1959a). Hickman & McLean (1990) summarised the history of treatment of these genera and concluded that the hylistylinae taxa are most appropriately treated as a derived trochid subfamily related to Lirulariinae and Umboniinae. These three subfamilies all have monopectinate ctenidia and radulae that lack fully developed rachidian and lateral teeth. Lirulariinae are restricted to the North Pacific and are one of the few trochoidean suprageneric taxa not represented in the Australian fauna; the subfamily is not treated here. Umboniinae (treated below) achieve maximum generic diversity and diversity of shell form in the Australian fauna.

The minute shells (Fig. 15.67A, B) are thick, sturdy, and lack visible nacre. Shell shape is either low and turbiniform, with rounded whorls and an open umbilicus (Fig. 15.67A), or elongate with a relatively straight-sided (pupiform) spire and no umbilicus (Fig. 15.67B). The aperture is prosocline and circular and the peristome is not interrupted. The outer lip is thickened within to form a characteristic rim inside the aperture that tapers to a sharp growing margin. Shell surfaces range from smooth to spirally sculptured and pigmentation ranges from uniform to variegated.

The external anatomy is poorly known; there are no observations on living or preserved animals of any of the Australian species. Observations of animals of *Halistylus* (Fig. 15.67C) show a relatively unspecialised epipodium with five pairs of short, stubby epipodial tentacles and undifferentiated neck lobes with entire margins. Cephalic lappets are absent. The position of the eye on the dorsal surface of the eye stalk is unique amongst trochoideans. The foot is relatively short and broad and is not bifid anteriorly as in the Lirulariinae and Umboniinae.

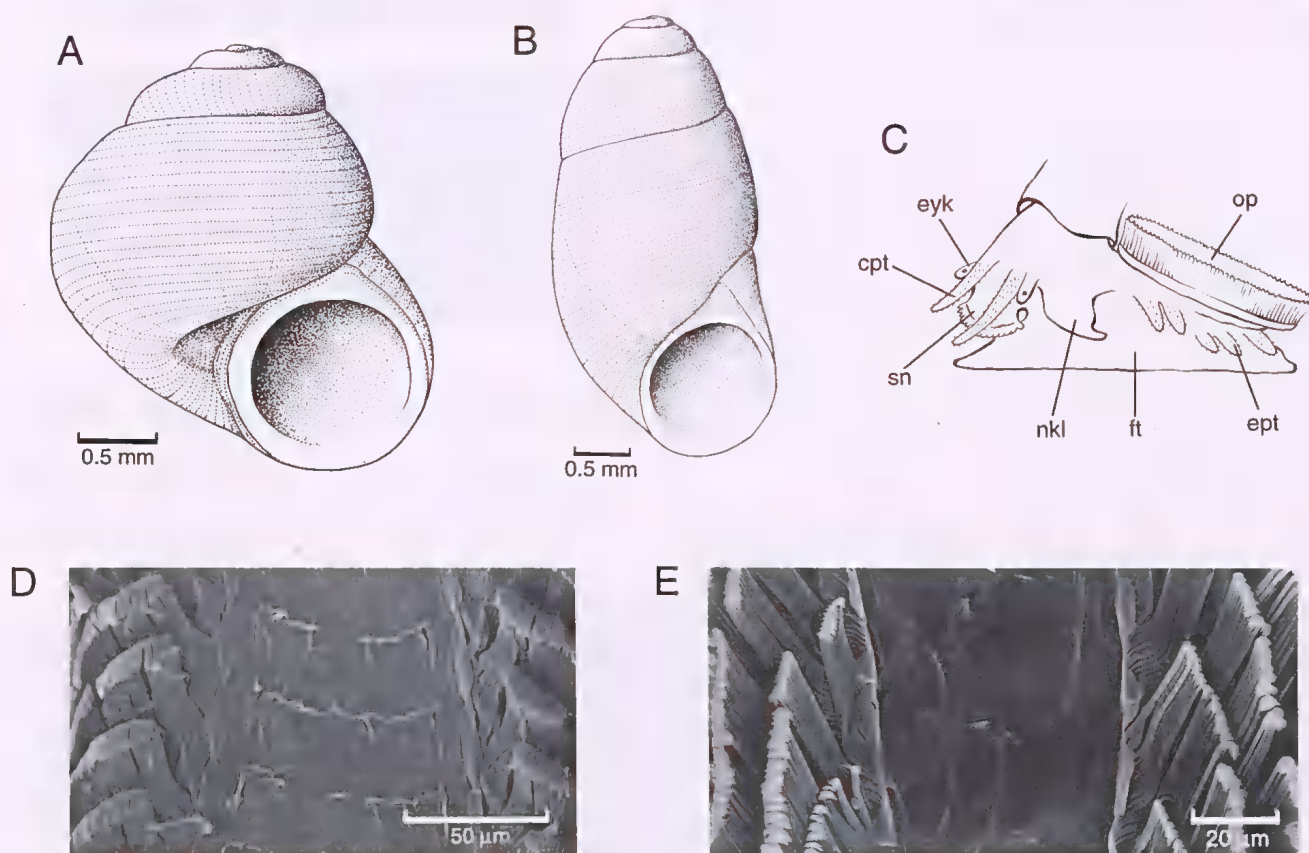


Figure 15.67 Family Trochidae, subfamily Halistylinae. A, B, shells, apertural view: A, *Charisma josephi*; B, *Botelloides bassianus*. C, *Halistylus pupoideus*, from the north-eastern Pacific, external features of head-foot. D, E, portions of radulae, showing all tooth types across several transverse rows: D, *Halistylus pupoideus*, from the north-eastern Pacific; E, *Botelloides bassianus*. cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk with eyes on the dorsal surface; ft, foot; nkl, neck lobe; op, operculum with upturned fringe; sn, snout. [A, B, S. Weidland; C, M.E. Taylor; D, E, G. Avern]

The snout (Fig. 15.67C) is broadened anteriorly and has a fluted fringe. It is not clear whether the fringe is in any sense homologous with the more highly developed tentacular fringe of solarielline gastropods or whether fringes and snout papillae are convergent adaptations in the trochoidean taxa that live on or in unconsolidated substrata. Major features of the halistyle radula are illustrated in Figure 15.67D, E. The radulae in all three halistyle genera are characterised by loss of structure in the central field. There are distinct columns of interlocking latero-marginal plates on each side of the undeveloped central field in *Halistylus* (Fig. 15.67D). The marginal teeth have delicate shafts and short cusps showing several different kinds of subdivision and serration; and basal fusion of marginal tooth shafts is common in all three genera (Fig. 15.67D, E). Nothing is known of either the diet or the feeding behaviour of any of the species in the subfamily.

Shells of halistyle species are most commonly recovered from relatively coarse sand subtidally on the continental shelf, and animals are inferred to live on, or interstitially in, unconsolidated substrata. Live animals are rarely collected. Ponder (1985b) provided detailed distribution maps for the living and fossil species of *Botelloides* in Australia. Geographic distributions of the Australian species tend to be either circum-Australian or, more typically, restricted to some portion of the southern half of the coastline. The genus *Charisma* is known exclusively from the southern half of Australia.

The austral halistyle lineage first appears in the Eocene of Victoria. The sturdy shells are well represented in the fossil record. Ponder (1985b) described the fossil species and subspecies of *Botelloides* and documented their stratigraphic and geographic distributions.

Subfamily Umboniinae

The Umboniinae are one of the most highly derived and easily diagnosed trochoidean subfamilies. The left neck lobe is modified into a particle exclusion filter that is a complicated tentacular meshwork in the most specialised filter-feeding taxa. Eyestalks are curved so that the large terminal eyes, often blue pigmented, face upward. The snout is reduced in size and covered with fine setiform papillae. The radula is reduced in size, and the rachidian and lateral teeth are lost except for thin basal plates with rolled edges. The anterior end of the foot is bifid, but of a form distinctly different from the anterior lateral processes of the solarielline foot.

Hickman & McLean (1990) have revised the concept of this subfamily and subdivided it into three tribes: the Monileini, Bankiviini and Umboniini. This revision brings together for the first time a group of austral genera previously not considered to be closely related. The broad range of shell morphologies within the Umboniinae has contributed to the failure to recognise the constituent taxa as a natural group. Eleven of the eighteen main genera in this subfamily are based on an Australian type species. Species of several of the endemic Australian genera are extremely abundant in the Australian fauna and dominant in certain habitats. Cotton (1959a) recognised 12 genera in the subfamily, including some that have been removed subsequently. He did not recognise *Bankivia* and its allies as umboniine, treating them instead as 'kelp shells' under the Cantharidinae. The Umboniidae have been treated as a separate family by a few authors (for example, Finlay 1927a; Golikov & Starobogatov 1975; Walsby & Morton 1982).

Herbert's (1992) monographic revision of the Umboniinae of southern Africa and Mozambique has provided valuable new data on umboniine external anatomy and radulae as well as important comparative data and illustration of Australian material.

The shells are minute (less than 5 mm high) to medium-sized (30 mm high) and vary from low-spined and lenticular to unusually narrow and high spined (Fig. 15.68A–F). The greatest variation in shell form is within the basal tribe, Monileini, in which there are several distinct clades of tropical small-shelled taxa, several distinct clades of medium-sized, spirally and axially

ornamented shells that are easily confused with solarielline shells, and several distinct clades of smooth, glossy shells. The shell of *Monilea* is illustrated (Fig. 15.68A, B) as typical of the basal tribe. Hickman is revising this tribe, which is currently polyphyletic, and intends to propose several new umboniine tribes based on taxa in the faunas of Australia and New Zealand. Shells in the derived tribes Bankiviini and Umboniini are less variable in form. The high-spined, glossy, polymorphically coloured shell of *Bankivia* (Fig. 15.68C, D) and its allies are among the most distinctive and abundant shells on some beaches in Australia. The relatively heavy, lenticular shells of *Umbonium* (Fig. 15.68E, F) with their characteristic heavy umbilical callus, are equally distinctive, but are rarely found in the Australian fauna. In all three tribes there are some distinctive colour polymorphisms that include various combinations of solid colours, spiral bands, blotches and zigzags in pink, brown, violet, dark purple and white.

The major features of umboniine external anatomy are illustrated in Figure 15.68G–I. Distinctive modifications of the epipodium are associated with some of the more distinctive shell forms. The neck lobes are strongly dimorphic, and the margin of the right neck lobe is modified into various tentacular subdivisions that screen the entrance to the mantle cavity. In the most highly derived infaunal members of the Bankiviini and Umboniini, the right neck lobe is capable of full enrolment into a tubular siphon with an elaborate terminal tentacular meshwork (Fig. 15.68H, I). There are four pairs of epipodial tentacles. The cephalic tentacles are of unequal length and asymmetrically placed in the most derived taxa. The setiform papillae on the snout differ in form from the terminal tentaculiform processes in the Solariellinae and are autapomorphic for the subfamily. The tubular snout tapers anteriorly to the small mouth and reduced oral disc. The bifid anterior end of the foot is likewise autapomorphic and the form of the foot lobes is distinct from the lateral processes of the solarielline foot. Rapid thrashing movement of the foot is an escape response common to members of the subfamily and results either in the shell rolling rapidly along the substratum or in swimming for short distances in the water column (Hickman 1985). The foot is used in rapid burrowing in the fully infaunal species.

The ctenidium is reduced to a fully monopectinate condition and the elongate filaments have swollen tips. The ctenidium is effective in removing suspended particles and is used for suspension-feeding in the most highly derived taxa. No examples of obligate suspension-feeding have been documented, however, and food is also acquired through selective deposit-feeding (Hickman 1985).

The major features of the umboniine radula are illustrated in Figure 15.68J, K. It is small relative to the size of the animal, and the rachidian and five pairs of lateral teeth are reduced to thin basal plates lacking shafts and cusps. Marginal teeth are well developed, with distinctive long overhanging cusps that are deeply serrated in the region proximal to the shaft. The radula is used to manipulate mucus-bound food strings during ingestion of material collected on the ctenidia and to manipulate and remove coatings from sand grains in several species. Feeding behaviour in *Umbonium vestiarium* was described by Hickman (1985), and other aspects of umboniine behaviour have been summarised by Hickman & McLean (1990).

The subfamily includes some intertidal taxa, but most species are restricted to environments below wave base. They live on or in sand, and a number of species reach peak population densities in or adjacent to major estuaries where water and sediments contain higher concentrations of particulate organic matter. Umboniine species occur around the entire Australian coastline, although species and genera can be divided into predominantly tropical taxa (for example, *Isanda*, *Ethalia*) and taxa that have radiated primarily at higher latitudes or in cooler, deeper water (for example, *Bankivia*, *Ethminolia*). Generic endemism is pronounced in this subfamily. *Bankivia* and *Leiopyrga* are only found in the Western Pacific and Australia; *Zethalia* and *Antisolarium* are endemic to New Zealand, and *Inkaba* is

15. PROSOBRANCHS

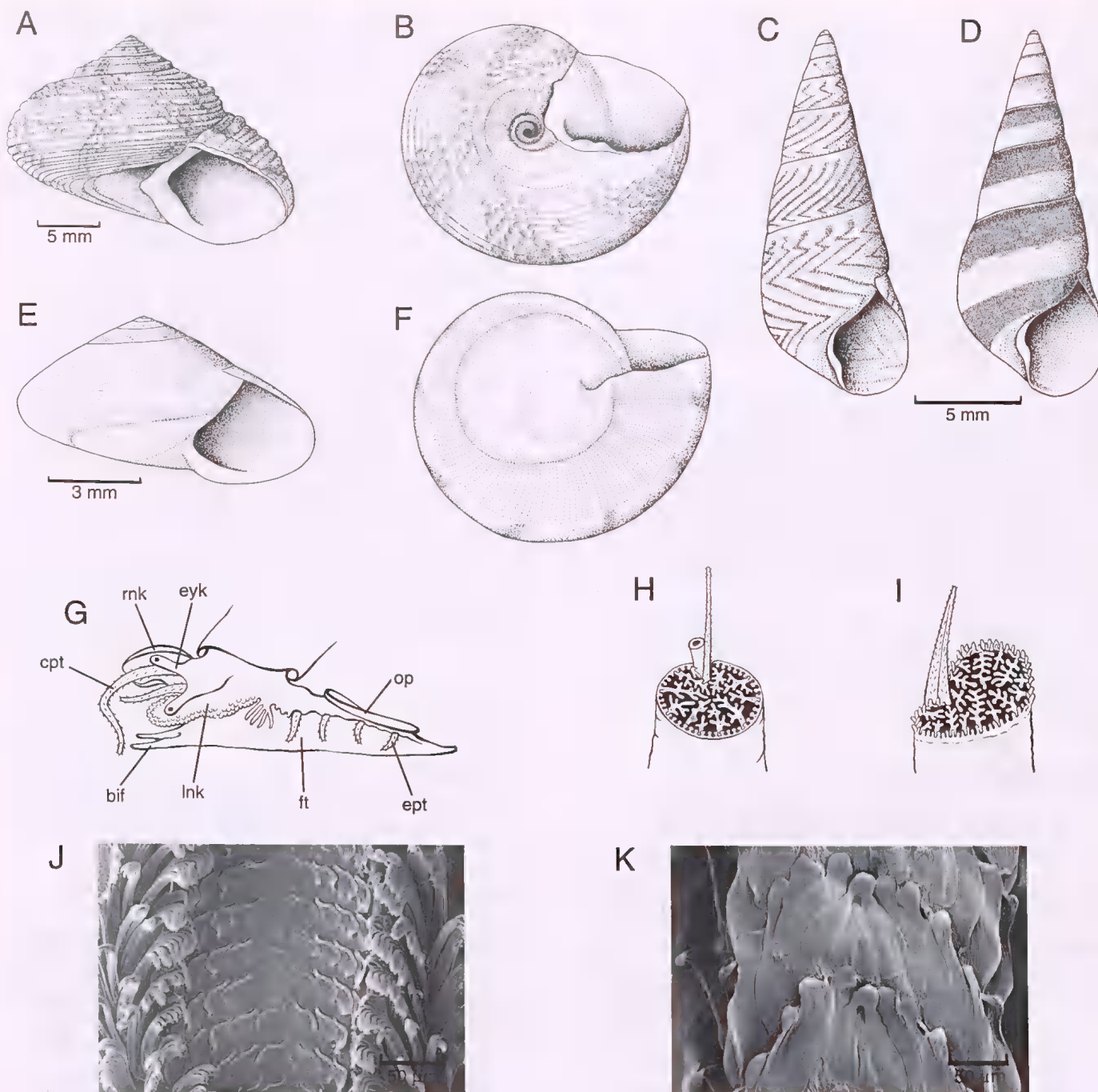


Figure 15.68 Family Trochidae, subfamily Umboniinae. A, B, *Monilea callifera*, shell: A, apertural view; B, umbilical view. C, D, *Bankivia fasciata*, shells showing two pattern morphs, apertural view. E, F, *Umbonium vestiariun*, shell: E, apertural view; F, umbilical view. G, *Umbonium moniliferum*, from Japan, external features of head-foot. H, I, enrolled inhalant neck lobes (right): H, *Umbonium vestiariun*, from Hong Kong; I, *Bankivia fasciata*. J, K, portions of radulae: J, *Bankivia fasciata*, several transverse rows; K, *Monilea callifera*, central field of several transverse rows. bif, bifid anterior end of foot; cpt, cephalic tentacle; ept, epipodial tentacle; eyk, eye stalk; ft, foot; lnk, left neck lobe; op, operculum; rnk, right neck lobe. [A–F, S. Weidland; G–I, M.E. Taylor; J, C.S. Hickman; K, G. Avern]

endemic to southern Africa. Although *Ethminolia* was once considered to be endemic to Australia, Herbert (1992) recently used the name to recognise affinities of species in southern Africa, Australia and Japan.

The subfamily has no major economic value, however, the shells of some species are used extensively in jewellery and folk art. *Bankivia fasciata* washes up on the south-eastern and southern beaches by the millions after heavy storms. It has sometimes been called the 'necklace shell' and in the Sydney area, shells were once used as weights around the margins of doilies that were placed over milk pitchers to exclude flies (Retallack personal communication).

The earliest unequivocal umboniine fossils are in Upper Cretaceous rocks, although there are some superficially similar lenticular shells in the Palaeozoic. In Australia, the subfamily is represented by abundant, well-preserved specimens in the Late

Tertiary and Quaternary of Victoria, South Australia and Western Australia. Eleven extinct species are named, including six species of *Leiopyrga* and an unusually large-shelled (greater than 30 mm) species, *Bankivia howitti*. There are a number of undescribed taxa in the Perth Basin, representing greater diversity of shell form than in the living fauna (C.S. Hickman personal observation).

Family Skeneidae

The Skeneidae are tentatively diagnosed by the combination of reduced shell size and loss of nacre, a type of monopectinate ctenidium that is distinct from that of other trochoideans, elongate epipodial tentacles with micropapillae uniquely arranged in lateral rows, and the capacity to develop a unique, prominent postoptic tentacle. Shell characters alone are insufficient to identify members of the family.

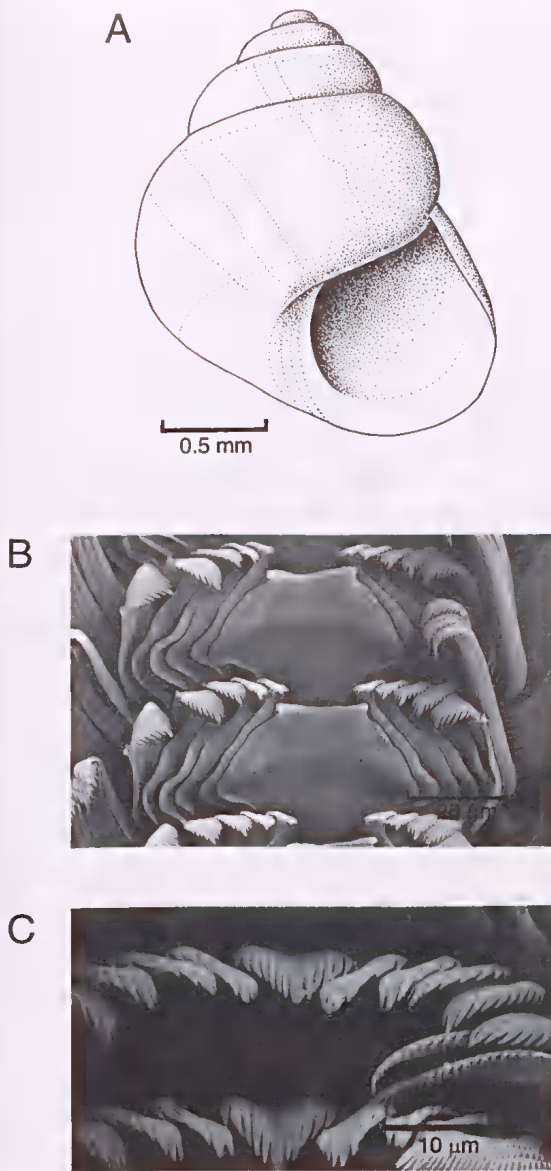


Figure 15.69 Family Skeneidae. A, *Putilla translucida*, shell, apertural view. B, C, several transverse rows of radulae: B, *Crosseola concinna*, showing rachidian, lateral and inner marginal teeth; C, *Putilla* sp., showing rachidian, and lateral teeth and cusps on marginal teeth.

[A, S. Weidland; B, C, G. Avern]

Skeneids currently constitute a large, heterogeneous, polyphyletic group of genera and species with relatively nondescript, minute (less than 5 mm high), unpigmented, conspiral shells. The group is in need of detailed systematic revision. Hickman & McLean (1990) presented an historical review of the group that included a reference to some of the family names that have been proposed (for example, Iredale & McMichael 1962) for minute Australian trochoidean and non-trochoidean shells. Ponder (1985a) identified a number of skeneiform taxa that have been treated incorrectly under Rissoidae. Traditionally, many of the Australian genera and species have been treated under Liotiidae (Lasercron 1954a; Cotton 1959a). Some of these taxa are small-shelled liotiines, and some of the others can be allocated elsewhere in the Turbinidae and Trochidae. Others have features that exclude them from any existing trochoidean family. Among the residual taxa are a few that seem to be related to *Skenea* and *Dikoleps*. Rubio-Salazar (1990), Ponder (1990a) and Warén (1991a) provided the first scanning electron micrographs of the shell and radula of the type species of *Skenea*, *Dikoleps* and a number of Atlantic and Mediterranean skeneiform species. There is some evidence of convergence in the North Atlantic species assigned to *Skenea*, and until this problem is sorted out, it is impossible to classify the Australian skeneiform taxa. Revision cannot be based on shells alone. It requires

examination of radular morphology and anatomy. Winston Ponder and John Healy are currently working on the morphology and sperm ultrastructure of some of the Australian taxa for which preserved specimens are available. The treatment below is a summary of the larger and, admittedly, polyphyletic group.

Shell morphology is highly variable in the skeneiform taxa. Figure 15.69A illustrates the shell of an Australian specimen tentatively assigned to *Putilla* (= *Notosetia*, = *Conicella*, = *Wanganella*), a genus that may be properly allocated to the Skeneidae *sensu stricto*. Shells range from thin and translucent to relatively thick and have surfaces that vary from smooth and glossy to spirally grooved or ribbed. Whorls are usually rounded, lacking a distinct peripheral demarcation. They may be umbilicate or nonumbilicate. The aperture may be entire or interrupted, and the outer lip is sometimes thickened and usually prosocline.

Data are lacking currently on the external anatomy of the Australian skeneiform species. The tentative diagnosis of the family is based on a combination of features of Atlantic species of *Skenea* and North American taxa that should probably be reassigned to Turbinidae on the basis of their radular morphology (C.S. Hickman personal observation).

Radular morphology is highly variable in the skeneiform taxa examined to date and provides stronger support than shell morphology for the contention that it is a polyphyletic group as presently constituted (Hickman & McLean 1990). The radular morphology of Australian *Crosseola* species (Fig. 15.69B) is of a turbinid plan and provides an example of one of the Australian skeneiform groups that is best removed from the Skeneidae. Figure 15.69C illustrates the radula morphology of an Australian *Putilla*, tentatively assigned to the Skeneidae. One problem with diagnosing and comparing skeneiform radulae is the reduction and simplification that occurs in many species, including the type species of *Skenea*, which shows considerable fusion of elements, both in the central complex and the marginals. Other North Atlantic species that have been assigned to *Skenea* have radulae suggestive of a modified turbinid or pseudococculinid plan. A second problem is that, even when well developed, the radula may have a strong component of morphological features that are generalised and characteristic of juvenile trochoideans (Warén 1990). This is consistent with the hypothesis that size reduction has occurred independently through heterochrony in many different trochoidean lineages.

There is no documentation of skeneid gut contents, diets, or feeding behaviour. It is probable, however, that the deep-water skeneids that have been recovered from wood and other biogenic substrata are feeding either on bacteria in the decaying wood or on surface films.

A consequence of their minute size is that skeneid shells and animals are not generally recognised in the field, but are subsequently sorted from samples. Most specimens in museum collections are empty shells. Live-collected animals are usually recovered from algal washings or from gravel under rocks or in crevices, indicating the kinds of habitats that warrant more careful systematic collection. Ponder (1990a) presented the first report of skeneids living interstitially in an intertidal gravel beach at Ceuta, southern Strait of Gibraltar. This report underscores the need to investigate these habitats more closely in Australia. In addition to the intertidal and shallow subtidal skeneiform taxa, there is a set of taxa associated with biogenic substrata in the deep sea. Marshall (1988b) provided a modern treatment of some of the taxa from bathyal depths off the New South Wales coast.

The more sturdy skeneiform shells are well represented from the Eocene to Holocene. There are many extinct species in the Tertiary basins of Victoria and South Australia, most of them undescribed (C.S. Hickman personal observation). Fossil specimens are under-represented in museum collections except where bulk sediment samples have been processed and sorted.

Family Pendromidae

This poorly understood family has been diagnosed (Warén 1991a) as having a distinctive net-like microsculpture on the early teleoconch, followed by a combination of spiral and axial sculpture on the later teleoconch. It is further diagnosed by loss of the radula and modification of the buccal mass to form a muscular cylinder. There are also unique details of external anatomy that are as yet incompletely documented. Warén (1991a) figured a specimen of '*Pendroma* sp.' from 1200 m off New South Wales, although the species remains undescribed. The degree of elaboration of the epipodium described by Warén (1991a) suggests trochoidean affinities, but insufficient is known about the group to allow full treatment here. The name is included to call attention to the presence of the group in the Australian deep-water fauna and the fact that what little is known of the taxon is based on an Australian specimen. Shells are minute (less than 5 mm high), and if represented in museum collections, they are probably filed with skeneids, miscellaneous minute trochids, or rissooideans.

The family name Trachysmatidae, which was based on an erroneously identified genus, is a junior synonym of Pendromidae.

Superfamily SEGUENZIOIDEA

This superfamily contains a single distinctive family of deep-sea gastropods that appears to have its closest affinities with trochoidean vetigastropods. Some authors have emphasised the distinctive aggregate of plesiomorphic and autapomorphic characters to argue for a taxon of subordinal rank, intermediate between Vetigastropoda and Caenogastropoda (Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a), whereas others argue the presence of synapomorphies that support inclusion in the Vetigastropoda (Quinn 1991; Haszprunar 1993). A number of reports of seguenzioid anatomical features in the literature have been discarded or reinterpreted as a result of re-examination of preserved material, and these are enumerated in the family treatment.

The most obvious functional differentiation between the Seguenzioidea and Trochoidea is that the anatomical specialisations for mantle cavity circulation in the Trochoidea are based on the elaboration of epipodial tissue to form semitubular neck lobes, whereas the specialisations in seguenzioids are based on elaboration of mantle tissue to form semitubular lobes (C.S. Hickman personal observation). Because the mantle serves the primary function of secreting shell the secondary function of channelling water also is reflected in the secretion of pronounced labral sinuses in many members of the subfamily. Additional shell features of the superfamily are discussed under the family treatment.

The origins of controversy in the interpretation of neritimorphaoid features can be traced to Verrill (1884), who described the radula as taenioglossate, leading some authors to treat them as mesogastropods. Quinn (1983a) summarised the history of systematic placement of seguenzioid gastropods. Authors who have treated them as archaeogastropods have recognised them either as a distinct trochoidean family or considered them to be trochids in the subfamily Margaritinae (Thiele 1929–1935; Wenz 1938; Cotton 1959a; Knight *et al.* 1960b). Increased attention to the group over the past ten years has more than doubled the number of genera and species, expanded the concept of the family, and stimulated interest in phylogenetic relationships within the group (Marshall 1983b, 1988c, 1991; Quinn 1983a, 1983b, 1987, 1991). In one recent treatment, Marshall (1991) recognised three subfamilies and subdivided one of these into two tribes. He further recognised 20 genera and 139 species in the family. In another recent treatment, Quinn (1991) recognised two subfamilies. Hickman & McLean (1990) excluded the family from the Trochoidea in their suprageneric revision, but subsequent examination of epipodial and ctenidial features (C.S. Hickman personal observation) suggests closer affinity with trochoideans within the Vetigastropoda.

In spite of the increased documentation of shell morphology and radular morphology, there are no observations to date on living animals and no thorough, illustrated anatomical studies. Most of the anatomical features that have been reported and generalised as characterising the entire group are not clearly tied to identified taxa, and comparative anatomical studies are especially desirable in view of the number of generic and suprageneric taxa currently recognised.

Family Seguenziidae

The family Seguenziidae is diagnosed by a combination of shell features including reduced shell size and thickness, having the nacre visible through the thin unpigmented calcitic layer, and shell sculpture. Seguenziids have the ability to produce several types of exceptionally fine, elaborate microsculpture, sharp delicate carinae, and as many as five complex labral notches and emarginations that are imperfectly reflected in fine growth lines on the shell.

Excellent illustrations are available in the literature of the adult shells, microsculpture, protoconchs, and other shell features of many seguenziid species (see especially Quinn 1983a; Marshall 1991). However, no synapomorphies have been recognised for seguenziid genera and subfamilies and considerable intergradation is seen in features that have been described. The lack of clear novel distinguishing shell features coupled with lack of knowledge of seguenziid internal anatomy makes it difficult to evaluate the taxonomic diversity of the family. Seguenziids are not well known in the Australian fauna at present. Five living Australian species can be assigned to the genera *Seguenzia*, *Basilissa* and *Calliobasis*. *Sequenzia polita* is the most common of the five in museum collections. The number of named Australian species is probably an underestimate of the taxonomic diversity in view of the large, newly described faunas from New Zealand (Marshall 1983b) and New Caledonia (Marshall 1991).

The shell of a typical seguenziid from the eastern Australian continental slope is illustrated in Figure 15.70A. Most seguenziid shells are easily recognised by their minute size, the peculiarly lustrous surface owing to the visibility of nacre through the translucent outer layer, the delicate microsculpture, and especially the elaborate labral sinuses. There is considerable variation in many shell features: the number and sharpness of whorl angulations (there is almost always a peripheral angulation, although shoulder angulations are absent in many taxa); the number and shape of labral sinuses; the presence or absence of a columellar tooth and the morphology of the tooth; the character of the microsculpture; the presence or absence of an umbilicus; the ornamentation of the umbilical area; the degree of thickening and reflection of the columellar lip; and the changes in microsculpture from protoconch to early teleoconch to later teleoconch. For discussions of variation in shell morphology see Quinn (1987) and Marshall (1991).

There is considerable variation in external features that have been reported to date, and because so few species have been examined, it is not safe to extrapolate the information summarised here to all seguenziids. The foot has an unusually well-developed and highly differentiated epipodium with as many as eight or nine pairs of slender epipodial tentacles that may vary in length and in number from one side of the animal to the other. The cephalic tentacles may also differ in length and in number from one side of the animal to the other. There is a right suboptic tentacle of unknown function. Cephalic and epipodial tentacles are densely covered with fine micropapillae as in trochoideans. Eyes, if present, are black and located at the bases of the cephalic tentacles rather than on eyestalks as in trochoideans. The snout may have lateral projections, analogous to those in some eucycline and solarielline trochids. Although a male copulatory organ with an open sperm groove has been reported for some seguenziids (Quinn 1983a; Haszprunar 1988a, 1988b), these structures are now known to be absent in others (Quinn 1991).

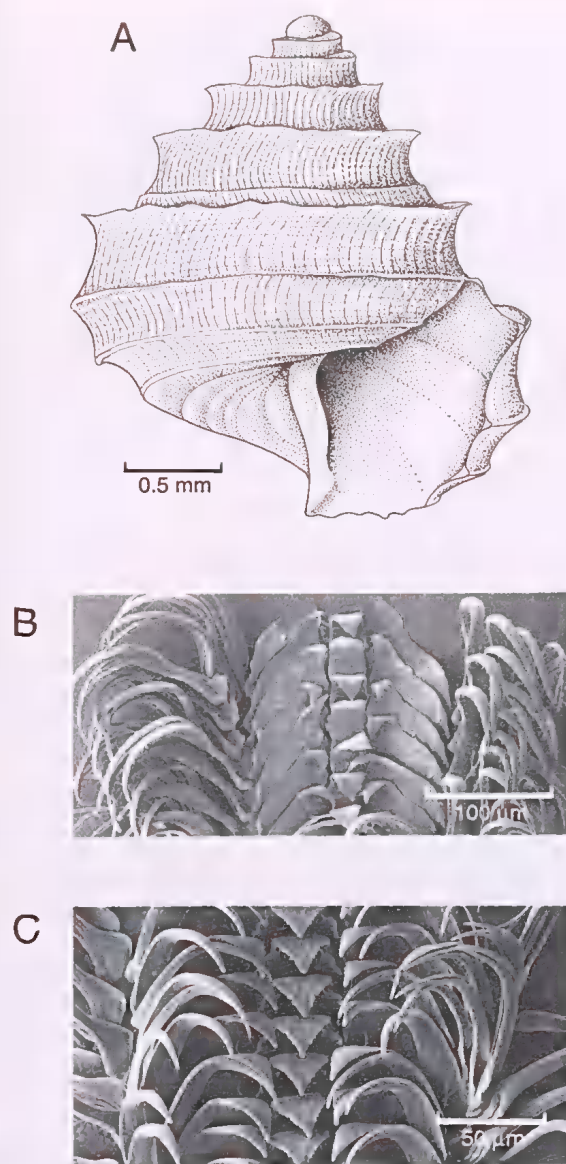


Figure 15.70 Family Seguenziidae. A, *Seguenzia* sp., shell, apertural view. B, C, several transverse rows of radulae: B, *Seguenzia megaloncha*, from the north-eastern Pacific; C, *Ganesa* sp. [A, S. Weidland; B, C, C.S. Hickman]

The mantle edge is sinuate and may have two major and two minor embayments corresponding with labral emarginations. These embayments may be micropapillate and some species have a distinct dorsal mantle tentacle. The two major embayments probably can be enrolled to serve the same function as trochoidean neck lobes, namely channelling water flow through the mantle cavity. The ctenidium has been characterised as monopectinate (Haszprunar 1988a, 1988b), but it does not have the modified elongate filament with swollen tips that characterises the suspension-feeding monopectinate ctenidium of derived trochids (C.S. Hickman personal observation). It does have the conspicuous sensory bursicles characteristic of trochoidean gastropods (C.S. Hickman personal observation), contrary to an earlier report of their absence by Salvini-Plawen & Haszprunar (1987).

Features of internal anatomy are least well known and most controversial, and the best summary of current knowledge is that of Quinn (1991). Salvini-Plawen & Haszprunar (1987) reported a single left kidney, but that has been revised to two (Haszprunar 1988b, 1993). The lack of oesophageal pouches reported by Haszprunar (1988a, 1988b, 1993) is questioned by Quinn (1991), who recognised vestigial pouches.

The major features of a generalised seguenziid radula are illustrated in Figure 15.70B, C. The radula is of a modified rhipidoglossate form characterised by reduction in the number of

lateral and marginal teeth. The rachidian is flanked by a single pair of laterals, and the four to twelve pairs of marginals fold over the central complex as in the trochoidean radula. The rachidian has a denticulate overhanging cusp, and the lateral has a broadly expanded base, thin short shaft and small overhanging cusp. There is no latero-marginal plate, but the inner marginal has a broader base than the other marginals, which are slender feathery teeth with finely denticulate cusps resembling those of eucycline trochids. Illustrations of seguenziid radular morphology are provided by Quinn (1983a), and scanning electron micrographs by Marshall (1991). The minute radula is fragile and difficult to prepare for microscopy, and some of the unusual morphologies illustrated in early literature are artefacts of preparation. Gut contents and the elongated, convoluted hindgut suggest that the animals are deposit feeders on very fine sediments.

Living seguenziids all occur in deep water and most are restricted to bathyal depths (primarily between 200 and 1000 m). They occur worldwide on fine sedimentary substrata. The anomalously low diversity of the Australian fauna, in contrast to the anomalously high diversity in New Zealand and New Caledonia, is difficult to explain, but it is probably partially a result of the lack of intensive sampling on the continental slope and shelf.

The fossil record of unequivocal seguenziid gastropods dates from the Late Cretaceous. In Australia, there are two described species from Neogene rocks and an undescribed species in the Eocene (C.S. Hickman personal observation). In spite of the delicate shell, specimens of the Australian Tertiary species are very well preserved. The family may have a Palaeozoic or Mesozoic origin, but it is difficult to determine relationships through homology of shell features. This is especially true of the labral emarginations that are the hallmark of the family. Labral emarginations have many independent origins in primitive marine gastropods and it is possible that emarginations were absent in the ancestral stock.

Superorder NERITOPSINA

This clade, also called Neritimorpha (for example, Haszprunar 1988a), includes only the Neritoidea, comprising Neritopsidae, Helicinidae, Hydrocenidae, Phenacolepadidae, Neritidae and Titiscaniidae, although the group has a long fossil history (Middle Devonian to Recent, Knight *et al.* 1960b). Although neritids and their relatives were considered to be very distinct from other 'archaeogastropods' by a few authors (for example, Bourne 1908; Yonge 1947; Morton, J.E. & Yonge 1964), they have been treated as merely a superfamily within the 'archaeogastropods' by most authors (Thiele 1925a, 1929–1935; Wenz 1938–1944; Knight *et al.* 1960b; Fretter & Graham 1962; Taylor, D.W. & Sohl 1962). Recently, in reviews of gastropod classification (Golikov & Starobogatov 1975; Haszprunar 1988a, 1988b; Bieler 1992a; Ponder & Lindberg 1996, 1997), the group has been recognised as a distinct clade.

Amongst the apomorphies shown by Neritopsina (many also shared with cocculinoideans, see Ponder & Lindberg 1997) are the lack of salivary glands, absence of a true jaw, paired diverticula from the sublingual pouch (Salvini-Plawen 1972) and oesophageal glands forming two separate glands. In addition, these molluscs lack shell nacre, have highly modified stomachs, a single (left) ctenidium and only the left kidney is functional. Possible plesiomorphic features include cone crossed-lamellar shell structure, lack of ctenidial skeletal rods, paired shell muscles divided into discrete bundles with blood sinuses passing between (also in patellogastropods and some lepetelloideans) and the rhipidoglossate radula, a feature shared with the Vetigastropoda.

The neritopsine larval shell is highly modified, possibly partly because of intracapsular development, but also because of a planktotrophic feeding phase. The protoconch is very distinctive (Fig. 15.72J; Bandel 1982), and is readily distinguished from those of other groups of gastropods.

15. PROSOBRANCHS

Members of at least two of the Neritopsina families, Neritidae and Helicinidae, have a very distinctive nervous system. The pedal cords have numerous cross connections and the pleural and pedal ganglia are fused, at least to some extent. The pleural ganglia are zygoneurous, the suboesophageal ganglion is fused with, or abuts, the right pleural, and the supra-oesophageal ganglion is fused to the left pleural ganglion. There is no osphradial ganglion – it also is probably fused (along with the zygoneurous fusing of the supra-oesophageal ganglion) to the left pleuro-pedal ganglion, given the origin of the (left) osphradial and ctenidial nerves from that ganglion (Bouvier 1887; Fretter & Graham 1962).

Little is known about the ontogeny and larval development of neritopsines and particularly of their organogenesis. Larvae of only a few taxa have been described.

How the Neritopsina are related to the rest of the orthogastropods is currently unclear. Haszprunar (1988a) argued that they are the sister taxon to the non-patellogastropod gastropods. Ponder & Lindberg (1997) obtained different topologies, depending on the assumptions they used; some agreed with Haszprunar's hypothesis and others placed Neritopsina as the sister to the hot-vent taxa (Neomophaloidea + Peltospiroidea), which in turn are the sister group to Apogastropoda (Caenogastropoda + Heterobranchia) (see Fig. 15.1C).

The group has undergone a major adaptive radiation. Shell morphology ranges from tightly coiled and conical to limpet-like to absent (Titiscaniidae), although, interestingly, no tall-spined shell forms appear to have evolved. Multiple terrestrial and freshwater invasions have occurred; two families, Helicinidae and Hydrocenidae, are exclusively terrestrial.

Superfamily NERITOIDEA

Typically, marine neritoideans have a low-spined shell with a swollen last whorl and a D-shaped or semicircular operculum. The radula is rhipidoglossate ($\infty+5+1+5+\infty$), with numerous small teeth, of which the outermost laterals are the largest. Only the left kidney and left ctenidium are present (Fig. 15.73B); the right kidney is incorporated into the distal reproductive system. All species are dioecious, with complicated genital ducts.

The Neritoidea is a diverse, cosmopolitan superfamily comprising probably less than 300 species in approximately 120 genera and subgenera (Vaught 1989), in six families. The Neritopsidae, Titiscaniidae and Phenacolepadidae are exclusively marine, the Neritidae has marine, estuarine and freshwater species, and the Hydrocenidae and Helicinidae are terrestrial. The Neritoidea has a principally tropical and subtropical distribution, with small numbers of species occurring in temperate areas. Although not rich in species, Australia has representatives of all six neritoidean families: nine genera and at least 35 species are known from brackish, freshwater and terrestrial habitats (Smith 1992). A single genus, *Monterissa* (Hydrocenidae), is endemic to Lord Howe Island (Iredale 1944), but all other genera extend into South-East Asia or the Western Pacific.

One neritoidean species, *Titiscania limacina* (Titiscaniidae), is shell-less, but all others are shelled. Terrestrial species have conical, globose to flattened shells. The marine species have low-spined shells which may be globose, patelliform or capuliform with a wide aperture. Marine shells are porcellaneous and those of intertidal forms are heavy, affording resistance to desiccation and protection from predators. In these marine groups the aperture is partially occluded by a shelf-like septum formed by the expansion of the columella. This septum is often ornamented with teeth, folds or pustules. Apophyses, where present, articulate with the shell septum. Many forms usually have thin shells in which the internal whorls may be resorbed. Some non-Australian members of the terrestrial Helicinidae (Ceresinae, Proserpininae) lack an operculum and the shell aperture is protected by teeth or lamellae (Thompson 1980).

The head bears a single pair of tentacles with eyes situated at the bases, and the foot typically lacks an epipodium.

Neritoideans are omnivores, detritivores, or herbivores, feeding on algae and diatoms. No species is known to be exclusively carnivorous. The generalised rhipidoglossate radula is adapted for grazing, and is flexible enough to follow the contours of the substratum and remove edible matter. Neritoideans lack jaws and salivary glands, but have buccal diverticula or pouches which are lined with glandular tissue, and paired oesophageal glands which lie along the oesophagus (Bourne 1908; Whitaker 1951; Fretter 1965).

The heart may have either two auricles or a single left auricle. The left kidney is functional, the right has lost its role in excretion and is incorporated into the genital duct (Fretter 1965). The mantle cavity of marine forms encloses a single left ctenidium, which is bipectinate, and two hypobranchial glands. The ctenidium is lost in terrestrial forms and respiration takes place directly across the highly vascularised surface of the mantle cavity.

The females may be monaulic, diaulic or triaulic (Bourne 1908), and the males often have a muscular cephalic penis. Neritoideans produce spermatophores which facilitate sperm transfer, fertilisation being internal. The eggs are enclosed in gelatinous capsules that are laid singly or are encased in a hardened, lenticular egg mass (Andrews, E.A. 1935). In marine forms, the larvae are planktotrophic (Bandel 1982), but in most freshwater and all terrestrial forms development is direct.

Neritoideans are among the most abundant gastropods on tropical and subtropical rocky shores, and several species may occur sympatrically. They can out-compete many other groups and their populations are controlled largely by density-related factors (Underwood 1976c). The ecology of the few subtidal species is unknown. Terrestrial species are found mainly in the wet or monsoonal tropics and subtropics where a warm, humid climate permits the pallial lung to function efficiently. They are arboreal or strongly calcicolous, and are most diverse in rainforests and on limestone in the West Indies, Central and South America (Thompson 1980) and South Asia (van Benthem Jutting 1948, 1959).

Neritoideans are of little current economic significance, although some species are eaten by humans. In many areas of the Pacific the more colourful shells are used for adornment, and in Hawaii necklaces and bracelets of kŭpe'e (*Nerita polita*) were emblems of mourning for the chiefs (Kay 1979). Freshwater species of the European and south-western Asian genus, *Theodoxus* (Neritidae), are intermediate hosts of trematodes (Abdel-Hafez & Ismail 1983), and it is likely that other neritoideans may also transmit parasites.

The fossil record extends back to the Middle Devonian (Knight *et al.* 1960b).

Family Neritopsidae

The Neritopsidae are a small family represented by two extant species, *Neritopsis radula* in the Indo-Pacific (including Australia), and *Neritopsis atlantica* in the Caribbean. Both species are exclusively marine.

The shell is pale in colour, dextral, globose, with a depressed to relatively high spire and a rapidly expanding last whorl (Fig. 15.71A, B). Sculpture is in the form of spiral cords which are crossed by growth lines, eventually forming spiral lines of beads. The ovate-round aperture is crenulated, the inner lip indented with a square notch (Fig. 15.71A), diagnostic for the family. Another diagnostic feature is the calcareous trapeziform operculum (Fig. 15.71C, D).

The radula (Fig. 15.71E) lacks a central tooth, and the laterals increase in size towards the edge. There are numerous marginals.

Neritopsis radula is widely distributed in the Indo-Pacific from Mauritius to Funafuti (Tuvalu) and Hawaii, and is known from scattered localities in northern Australia. It is found in deep water

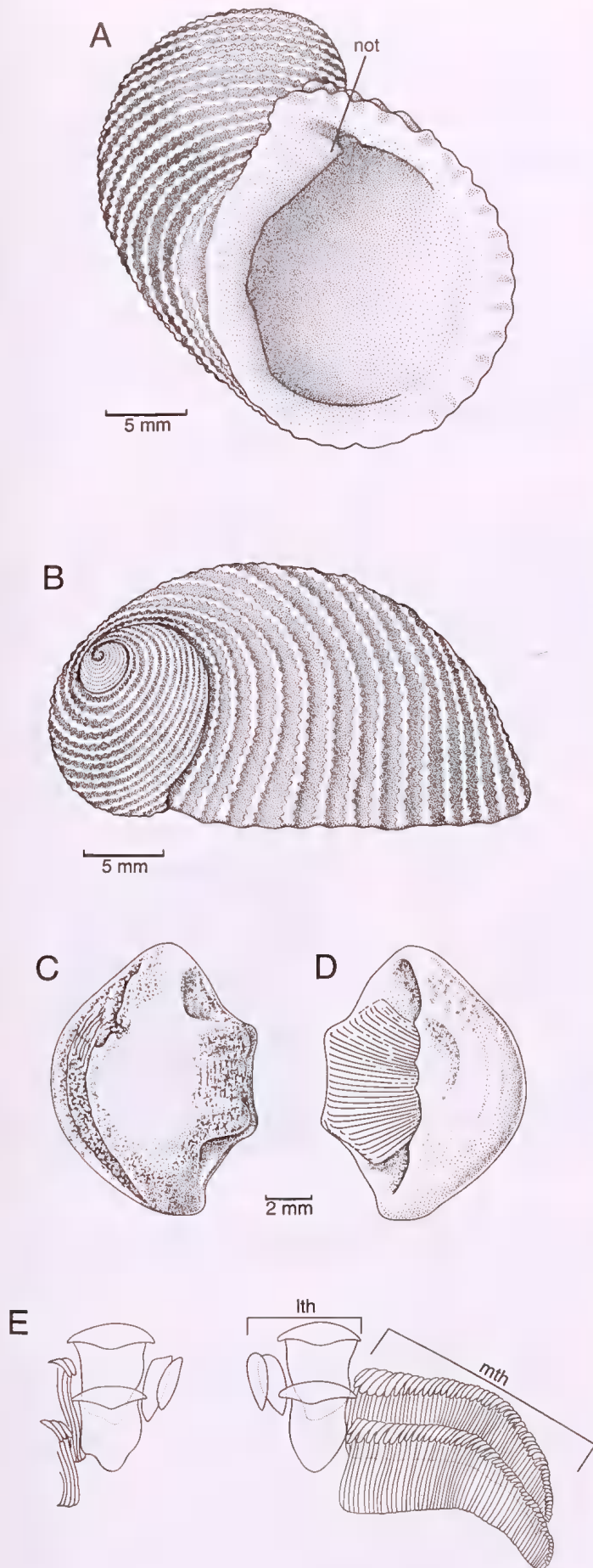


Figure 15.71 Family Neritopsidae. *Neritopsis radula*: A, apertural view of shell; B, lateral view of shell; C, D, operculum showing the outer (C) and inner (D) surfaces; E, two partial transverse rows of the radula showing the lateral teeth and marginal teeth on one side – note that the central tooth is lacking. lth, lateral teeth; mth, marginal teeth; not, square notch. (C, D, after Fischer 1880–1887; E, after Troschel (& Thiele) 1856–1893)

[A, B, C, Eadie; C, D, R. Plant; E, I. Hallam]

in Hawaii (Kay 1979), but has been recorded from marine caves on reef slopes in shallow water (0–40 m) off the Ryukyu Islands in southern Japan (Kase & Hayami 1992). Kay (1971) recorded it as being common as an empty shell in beach drift in the central Pacific. It has also been found living deeply embedded in coral rubble in sublittoral situations. Nothing is known of living neritopsids; their anatomy and biology remain undescribed.

Little is known of the Recent Neritopsidae, but this is the oldest family in the Neritoidea, the earliest recorded occurrence being from the Mid-Devonian of Europe. Many fossil ‘genera’, such as *Peltarion*, *Cyclidia*, *Scaphandria* and *Rhynchidia*, have been described on the basis of distinctive opercula (Knight *et al.* 1960b). Hoerle (1974) speculated on the evolutionary history of the Neritopsidae and the relationships of the Recent species.

Family Neritidae

Members of the Neritidae are common on intertidal rocks and mangroves on tropical and subtropical coasts worldwide, with a few on warm-temperate shores (Pl. 23.3). They also occur in brackish-water habitats and in freshwater. Two neritid subfamilies, Neritinae and Smaragdiinae, occur in Australian waters. The Australian Neritinae are represented by at least 20 species in the genera *Nerita*, *Neritina* and *Clithon*; most are from marine habitats, but one is restricted to freshwater streams and several others occur in estuaries, brackish-water and freshwater (Smith 1992; Wilson 1993). Australian Smaragdiinae are represented by four species of *Smaragdia* (Loch 1994), including *Smaragdia trigena*, from New South Wales and Queensland (also from Papua New Guinea) (Iredale 1936a; Wilson 1993; Loch 1994). Many of Australia’s marine and brackish-water neritines have a wide range along the northern coast from Western Australia and the Northern Territory to Queensland and New South Wales. These include *Nerita balteata*, which occurs on mangroves, and *N. albicilla*, *N. polita* and *N. undata*. Three species, *N. costata*, *N. grossa* and *N. planospira*, are widely distributed in the Indo-West Pacific, but are known in Australia only from Queensland. *Nerita atramentosa* (Fig. 15.72C, D) is found in southern waters, where it is common on rocky shores from southern Queensland round the south to the North West Cape, Western Australia, and including Lord Howe Island and Norfolk Island (Wilson 1993). It is also found in New Zealand and the Kermadec Islands (Powell 1979).

Australia has few neritid species in its freshwaters compared with other areas of the Pacific. New Guinea and Fiji each have 23 species, whereas areas adjacent to Australia, such as the Solomon Islands, Vanuatu and New Caledonia are inhabited by 14 to 18 species (Haynes 1988 and references therein). The freshwater genera *Neritilia*, *Neritodryas* and *Septaria* are not found in Australia, although they occur in South-East Asia, New Guinea and the Western Pacific (Haynes 1988).

Three species of *Neritina* are found in both brackish- and freshwater in northern Australia: *Neritina pulligera*, widespread in the Indo-Pacific from India and Africa to Fiji and the Philippines; *Neritina variegata*, ranging from India, South-East Asia to Samoa, Fiji and Tahiti; and *Neritina violacea*, also found in India, Western Pacific to Samoa and Fiji. *Clithon oualaniensis* also occurs in both brackish- and freshwaters of South-East Asia, and most of the Pacific. These species were discussed by Benthem Jutting (1956) in his study of Javanese freshwater gastropods. Only the poorly known *Neritina sulcata* is apparently restricted to freshwater in Australia (Smith 1992).

The shell (Fig. 15.72) is usually heavy and porcellaneous, and may be globose, turbiniform, capuliform or patelliform. The last whorl is inflated, the columella thickened and expanded to form a septum extending across the aperture. This septum may bear folds, teeth or papillae. Shells are often brightly coloured or strikingly marked, and may be ornamented with spines. Several species exhibit variation in shell colour. The Indo-Pacific species *Clithon oualanensis* (sometimes referred to as *Theodoxus oualanensis*), for example, demonstrates pseudopolymorphism (Fig. 15.72H, I; Grüneberg

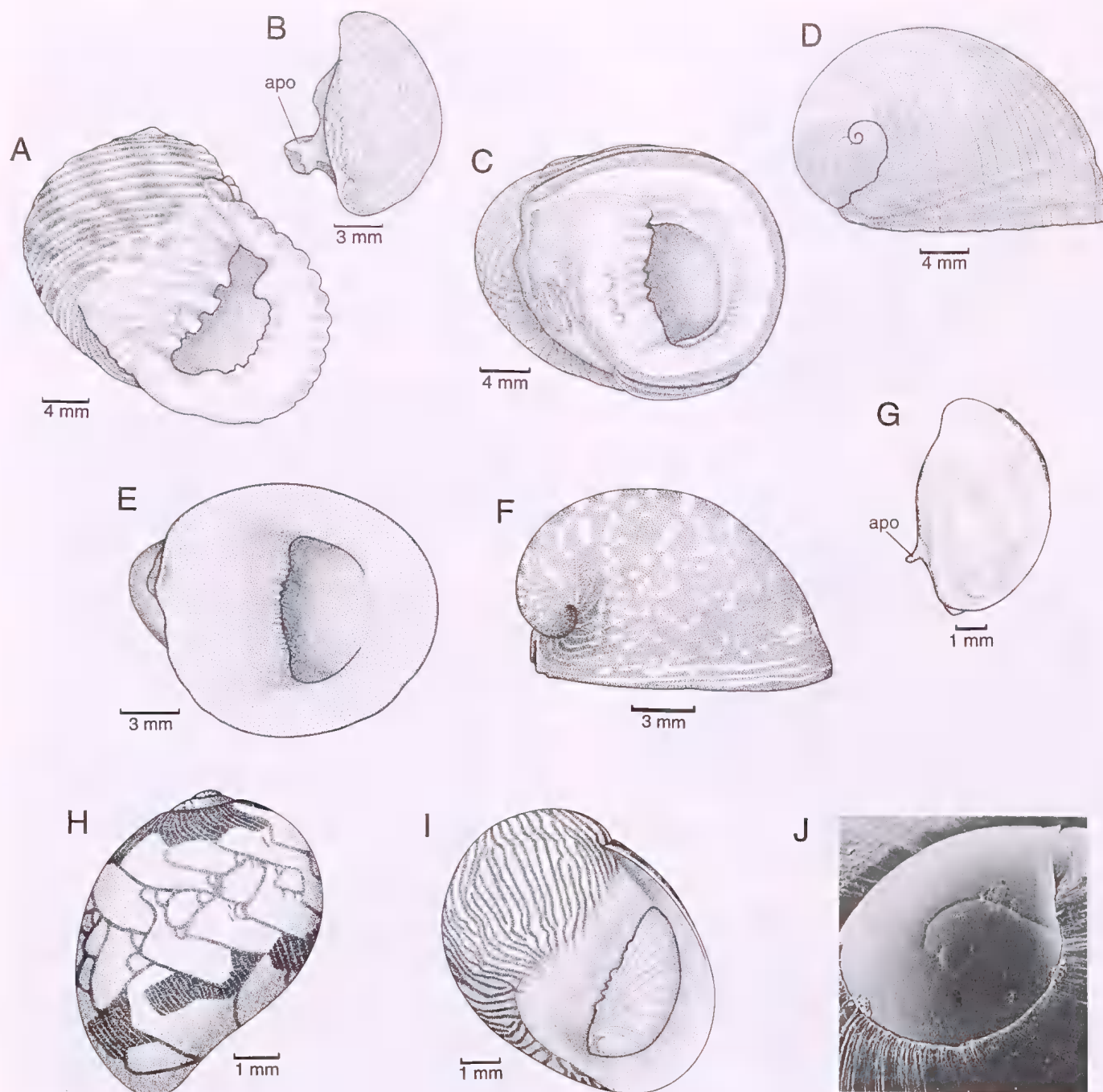


Figure 15.72 Family Neritidae. A, B, *Nerita plicata*: A, shell, apertural view; B, operculum, showing the outer surface and apophysis. C, D, *Nerita atramentosa*, shell: C, apertural view; D, lateral view. E–G, *Neritina violacea*: E, shell, apertural view; F, shell, lateral view; G, operculum, showing the outer surface and apophysis. H, I, *Clithon oualaniensis* shell, showing two colouration patterns: H, dorsal view; I, apertural view, with operculum in place. J, *Nerita*, protoconch – note that the larval shell covers much of the embryonic shell. apo, apophysis. (J, from Bandel 1982) [A–I, C. Eadie]

1982), a condition in which the different colour patterns appear to be discrete, but actually vary continuously. A study of the tropical western American species, *Nerita latissima*, in Costa Rica revealed that ingested manganese is incorporated into the shell material, resulting in dark shells on manganese-rich substrata (Valdez & Briceno 1980). The distinctive protoconch is illustrated in Figure 15.72J: it is strongly convoluted and ‘successive whorls (up to three) may completely cover the whorls formed before’ (Bandel 1982).

Shell shape can be variable in some species. Murty & Rao (1978) showed that the shells of the Indo-Pacific species *Neritina violacea* from protected mangrove habitats are broad with a narrow, centrally placed aperture, whereas shells from more exposed areas are narrower, with a wide posterior aperture.

Work by Gainey & Wise (1980) on the Caribbean species, *Nerita versicolor* and *Nerita tessellata*, showed that neritid shells comprise three layers: an outer prismatic layer (calcite), a crossed

lamellar layer (aragonite) and a complex crossed-lamellar layer (aragonite). This latter layer is covered with inclined platelets which may interact with the folds of the mantle to form a ratchet mechanism for mantle extension. An apertural ridge is also present, acting as a barrier against desiccation.

The operculum is semicircular (Fig. 15.72B, G). Its inner surface usually bears a peg-like apophysis and its inner margin articulates with the septum. The morphology of the operculum is important in diagnosing the subfamilies.

The mantle cavity has a bipectinate left ctenidium and a right ctenidium which is reduced to a small vascular knob (Fig. 15.73B; Fretter & Graham 1962). A right hypobranchial gland is present and a left hypobranchial gland may be present in some taxa (Fretter 1965). The mantle cavity floor of *Nerita* acts as an accessory respiratory surface (Fretter 1965).

The foot of the Caribbean species, *Neritina reclivita*, is composed of three groups of muscles: longitudinal, transverse, and diagonal. Three sets of mucocytes are also associated with the foot – anterior, epithelial and subdermal – releasing mucus during locomotion. Movement is achieved by the combined action of the transverse and longitudinal muscles, resulting in retrograde monotaxic waves (Gainey 1976). The neritid foot lacks an epipodium.

Neritids are mainly herbivorous, grazing on algae. The widespread temperate Australian species *Nerita atramentosa* has been recorded to feed on the patina of diatoms and algal spores on intertidal rocks, a food source that is replaced at every high tide (Underwood 1976c). The non-marine forms such as species of *Theodoxus* are omnivorous, with animal foods such as black fly larvae recorded in the diet (Pavlichenko 1977). The neritid radula is large with a small, square central tooth, four laterals, and numerous marginals (Fig. 15.73A; see Baker 1923). The radula may be of significance in distinguishing between genera (Lupu 1979).

The oesophagus is narrow and simple (Fig. 15.73C). Each oesophageal gland is a blind sac covering the posterior part of the odontophore, and attaches to the radular sac and not the gut. The oesophagus passes over the left oesophageal gland as it begins rotation through 180° (Fretter 1965). The sublingual pouch is situated under the buccal mass, its posterior wall supported by a plate of cartilage (Whittaker 1951; Fretter 1965).

The female reproductive system is complicated, and is either diallic or triaulic. In a few species the vaginal channel is separated from the pallial oviduct, resulting in two openings to the mantle cavity (Figs 15.22B, 15.73D). Structures associated with the vaginal channel include a bursa copulatrix or spermatophore sac and a seminal receptacle (Fretter & Graham 1962). Some neritids are triaulic, having a third duct, the ductus enigmaticus (Bourne 1908), related to the bursa and receptaculum, which carries waste to the mantle cavity. Houston (1990) in his study of reproductive systems of neritopsines from the eastern Pacific detailed that of *Nerita funiculata* (see Fig 15.73D). Hochpöchler (1981) studied the development of the female reproductive tract in the Central American species *Neritina punctulata*. Newly hatched animals have an ovary with few acini. A short non-pallial oviduct leads to the right inner end of the mantle cavity, opening through a primary genital opening. From there the pallial oviduct, which is a furrow in the mantle tissue, leads to the edge of the mantle, terminating as a secondary genital opening. Longitudinal divisions of the embryonic pallial gonoduct give rise to the pallial oviduct, whereas the oviducal glands are formed from its subepithelial cells. The vagina gives rise to the bursa copulatrix.

Males have a muscular cephalic penis on the right side. The vas deferens in *Theodoxus* species is not directly connected to the penis; sperm travel along a groove in the mantle wall (Fretter 1946). Spermatophores may be club-shaped (Bourne 1908) in the form of a loop, which is thick in the middle and thin at each end. A row of chitinous triradiate spicules twists around one end (Andrews, E.A. 1936). Females are either diallic or triaulic, and have a bursa copulatrix or spermatophore sac which receives the spermatophore during copulation. The sperm structure of various species of neritids has been examined (Giusti & Selmi 1982b; Selmi & Giusti 1983; Kohnert & Storch 1984c). The morphology of the neritoidean sperm cells differs markedly from other gastropods. Euspermatozoa of *Neritina* species have a pointed conical acrosome with an acrosomal rod, an elongate head, and only two mitochondria in the middle section (Kohnert & Storch 1984c). In the European species *Theodoxus fluviatilis*, euspermatozoa have an unusual flagellar structure. During spermiogenesis the flagellum folds in half giving rise to a tail with a double axoneme. The motility of these sperm is abnormal, with the tail preceding the head (Giusti & Selmi 1982b). Paraspermatozoa in *Theodoxus fluviatilis* are anucleate (Selmi & Giusti 1983).

During copulation exogenous sperm are deposited in the bursa copulatrix. They subsequently migrate via the ductus enigmaticus to the seminal receptacle, where they orientate with the heads projecting into the lumen (Fretter 1946).

Most marine neritids lay flat ovoid egg capsules on rocks or shells (Fig. 15.26A, B). The white, brittle capsule is about 2 mm long and consists of small calcareous spheres embedded in a matrix of the same material (Hedley 1917; Anderson, D.T. 1962). The capsule is filled with a jelly in which are embedded yolky eggs (Fig. 15.73E). Fertilised eggs bear a protective coat secreted by the capsule gland. A 'reinforcement sac' or 'crystal sac' receives material from the faeces and passes it on to the capsule gland; this material improves the strength of the egg capsule (Andrews, E.A. 1935; Fretter 1946). *Theodoxus fluviatilis* lays numerous eggs, most of which serve as food for a single juvenile (Bondesen 1940; Fretter 1946).

Life-cycles of neritids are not well-known. *Nerita atramentosa* has no real resting phase, although spawning is mainly a summer event (Underwood 1975a). Immature oocytes are present throughout the year, while the accumulation and storage of mature oocytes take place over a six-month period.

Nerita atramentosa larvae hatch after 14 days, and spend a short time as planktotrophic veligers (Fig. 15.73F, G; Anderson, D.T. 1962; Bandel 1982). Underwood (1975a) recorded settling of *N. atramentosa* larvae in May (late autumn), by which time the larval shell length had increased from 0.2 mm (Anderson, D.T. 1962) to 2.9 mm. The larvae of Hawaiian endemic *Nerita granulosa* migrate from salt water into river systems to settle on boulders in fresh water (Ford 1979). Development time of the brackish- to freshwater species *Theodoxus fluviatilis* depends on water temperature: development takes 65 days at 20°C, but only 30 days at 25°C (Fretter 1984b).

Nerita atramentosa reaches reproductive maturity at 20 months, after which growth ceases. Under normal circumstances mortality is negligible among juveniles, but is high among adults. The life span of *Nerita atramentosa* is between three and five and a half years (Underwood 1975a).

The growth rate of juveniles of *Nerita atramentosa* decreases as the population density increases. By artificially manipulating populations, Underwood (1976c) found that weight increase and growth stopped at densities of five times the field level. Adults are more susceptible to crowding, and weight loss begins at twice the average density. This phenomenon occurs when adults and juveniles are mixed, so the number of individuals is the important factor, not the age classes. Juveniles tend to live at higher shore levels than older individuals, resulting in shore-level size gradients (Chilton & Bull 1984).

Neritids ('nerites') are mainly inhabitants of the intertidal zones of rocky shores, where they are often the dominant gastropods. Wells (1978) found that three neritid species comprised almost 75% of all epifaunal macro-gastropods on a study site in the Admiralty Gulf, northern Western Australia. Neritids also occur on mangroves, and Berry (1964a) found that *Nerita birmanica* and *Nerita planospira* were so abundant on the lower tree zone of mangrove forests in Singapore that it was possible to use them as zonation indicators.

Neritids are usually active only when wet or washed by rising or falling tides, remaining inactive when wholly exposed or submerged. During daytime exposure, most individuals hide in crevices of rock pools, or cling to vertical surfaces. Few are found on slopes or horizontal surfaces. Neritids reduce heat stress mainly by clustering, but also by evaporative cooling (Garrity 1984).

Clustering behaviour is very common. Chelazzi, Deneubourg & Focardi (1984) found that during the neap tide–spring tide–neap tide cycle, about 90% of individuals in populations of the Indo-Pacific species, *Nerita textilis*, are found in clusters. Around 76% of individuals return to the original cluster after the first feeding excursion, but this number decreases markedly as the

15. PROSOBRANCHS

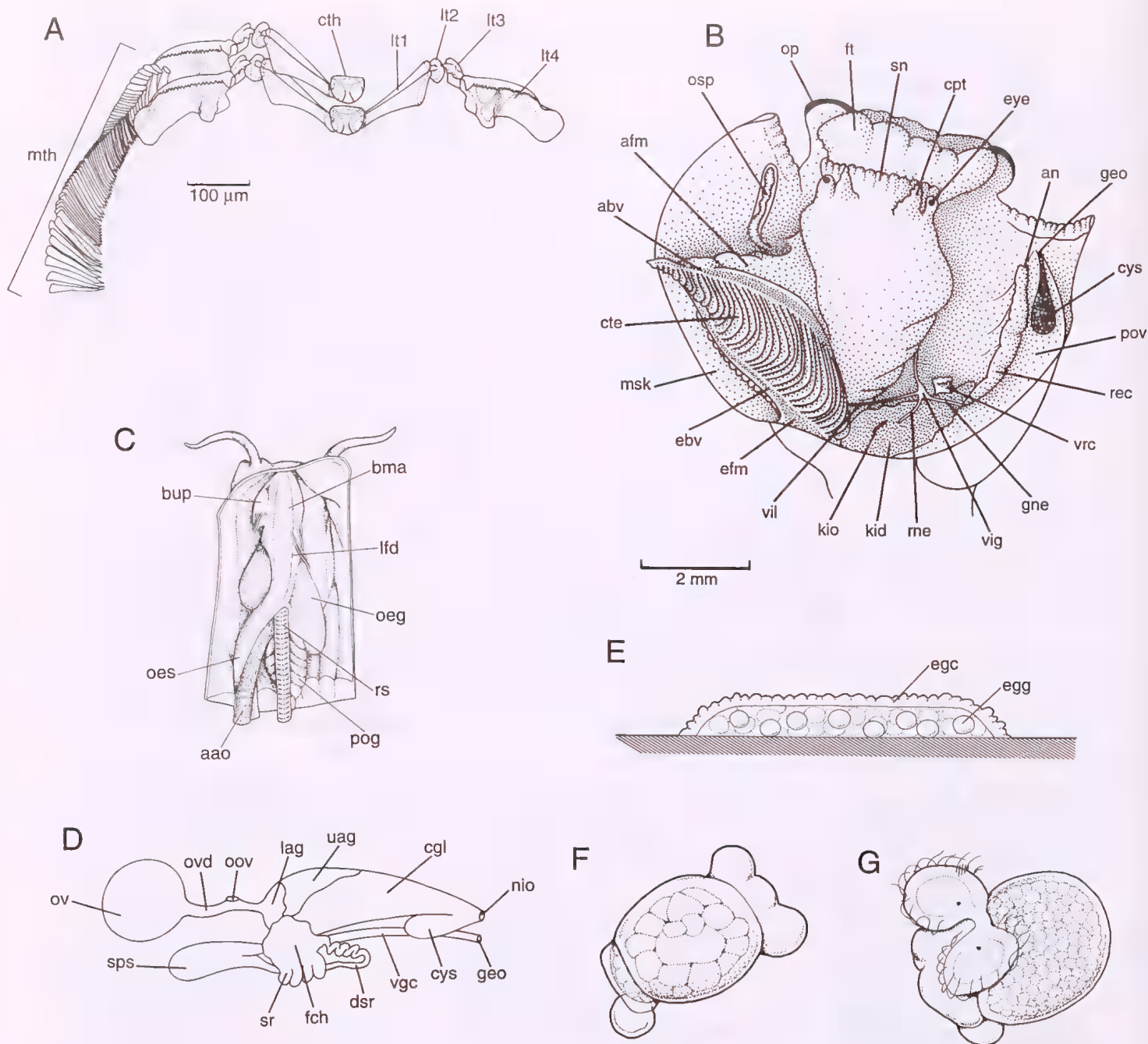


Figure 15.73 Family Neritidae. **A**, *Neritina virginia reclinata*, central and lateral fields and left marginal field of one transverse radular row; the left central and lateral fields of the next anterior are included to show relationships of teeth. **B**, *Theodoxus fluviatilis*, dissection of mantle cavity. **C**, buccal cavity, anterior and mid-oesophageal region of *Nerita* sp., dorsal view, showing position of oesophageal glands. **D**, *Nerita funiculata*, female genital tract. **E–G**, *Nerita atramentosa*: **E**, section through egg capsule showing eggs embedded in a jelly matrix; **F**, veliger at 5 days; **G**, veliger at 10 days. aao, anterior aorta; abv, afferent branchial vessel; afm, afferent membrane of ctenidium; an, anus; bma, buccal mass; bup, buccal pouch, glandular; cgl, capsule gland; cpt, cephalic tentacle; cte, ctenidium; cth, central tooth; cys, crystal sac; dsr, duct of seminal receptacle; ebv, efferent branchial vessel; efm, efferent membrane of ctenidium; egc, egg capsule wall; egg, eggs in egg capsule; eye, eye; fch, fertilisation chamber; ft, foot; geo, genital opening; gne, genital nerve; kid, kidney; kio, kidney opening; lag, lower albumen gland; lfd, longitudinal fold bordering dorsal food channel; lt1, lt2, lt3, lt4, lateral teeth, one to four; msk, mantle skirt; mth, marginal teeth; nio, nidamental opening; oeg, oesophageal gland; oes, oesophagus; oov, opening of oviduct into mantle cavity; op, operculum; osp, osphradium; ov, ovary; ovd, oviduct; pog, posterior part of right oesophageal gland attached to radular sac; pov, pallial oviduct; rec, rectum; rne, renopericardial nerve; rs, radular sac; sn, snout; sps, spermatophore sac; sr, seminal receptacle; uag, upper albumen gland; vgc, vaginal channel (sperm duct); vig, visceral loop; vil, part of visceral loop; vrc, vestigial right ctenidium ('organe creux' of Lenns). (A, after Baker 1923; B, after Fretter & Graham 1962; C, after Fretter 1965; D, after Houston 1990; E–G, after Anderson, D.T. 1962) [A, D, I. Hallam; B, C. Eadie; C, E–G, B. Scott]

number of excursions increases, particularly if an individual has one or more solitary rests. Clusters form lower down the shore during neap tides than they do during spring tides. There may be some chemical marking of the sites during the neaps, and trail-following results in progressive recruitment to the clusters.

Experimental crowding of *Nerita atramentosa*, *Cellana tramoserica* (Patellidae) and *Bembicium nanum* (Littorinidae) showed that the neritid was competitively superior and resisted crowding (Underwood 1978). Resource partitioning permits several neritid species to occupy an area of rocky shore. Although they are usually found in species pairs, three or four species may

occur sympatrically (Wells 1978, 1979). The Central American species *Nerita funiculata* and *Nerita scabricosta* are found together. *Nerita funiculata* is restricted to crevices on the mid-shore. It is active for short periods on rising or falling tides, when it forages up to 500 mm from its base. As a result of this the rock in a 100 mm radius is totally denuded of algal cover. *Nerita scabricosta*, by contrast, rests at high tide level and moves down the shore as the water recedes. The effects of its grazing extend to the whole intertidal community: patterns of barnacle settlement, density and size structure of sympatric *Nodilittorina* species (Littorinidae), and abundance of crustose algae are affected (Levings & Garrity 1983).

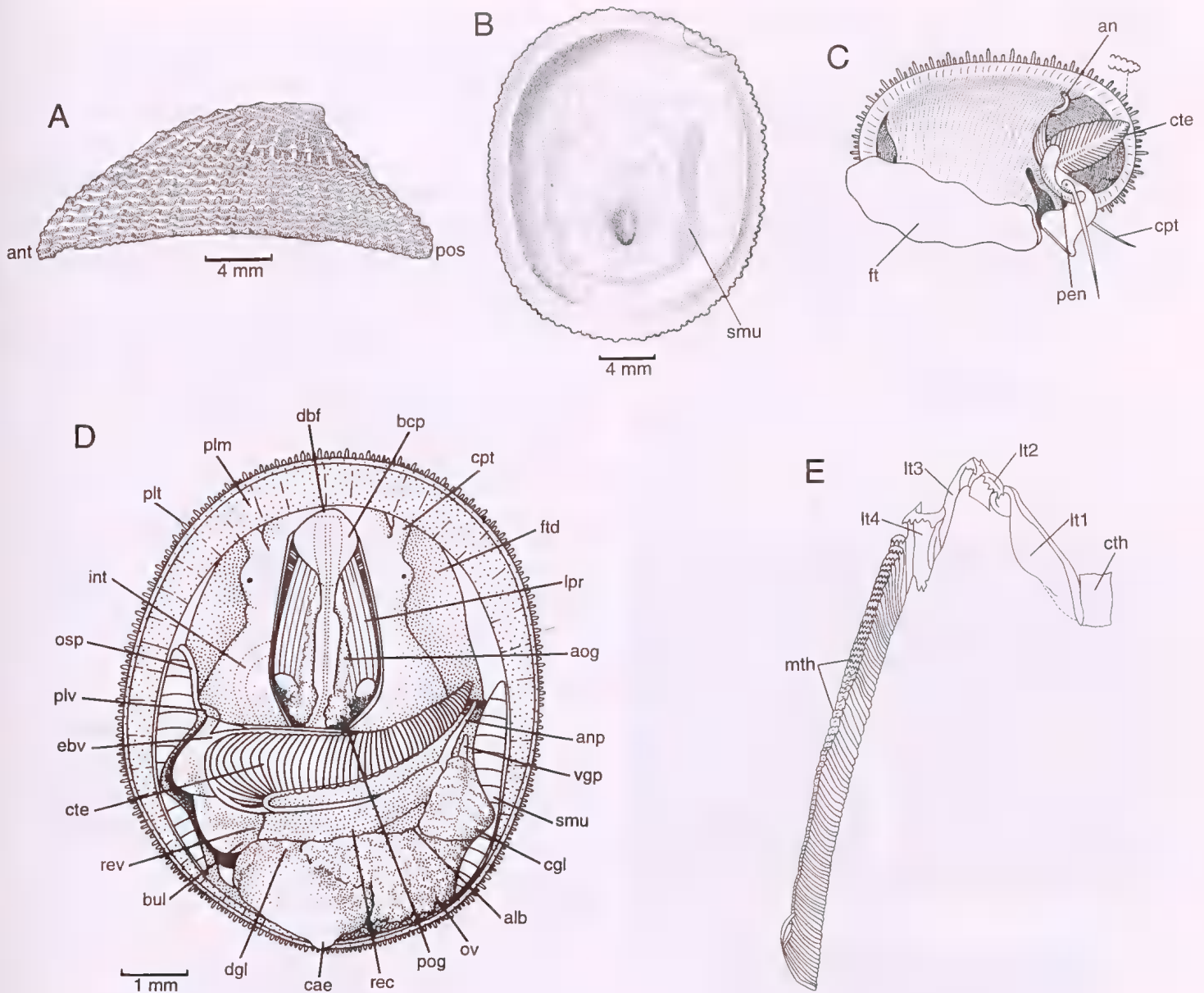


Figure 15.74 Family Phenacolepadidae. **A, B**, *Phenacolepas mirabilis*, shell: **A**, lateral view; **B**, ventral view, showing the horse shoe-shaped muscle scar. **C**, *Cinnelepete cinnamomea*, external features. **D**, *Phenacolepas omanensis*, a contracted female, dorsal view, with the shell and most of the mantle skirt removed, and the haemocoel opened mid-dorsally. **E**, *Olgasolaris tollmanni*, half of one transverse radular row. **alb**, albumen gland; **an**, anus; **ant**, anterior; **anp**, anal papilla; **aog**, anterior oesophageal gland; **bcp**, buccal pouch; **bul**, bulbous aorta arising from ventricle; **cae**, caecum of stomach; **cgl**, capsule gland; **cpt**, cephalic tentacle; **cte**, ctenidium; **cth**, central tooth; **dbf**, dorsal buccal fold; **dgl**, digestive gland; **ebv**, efferent branchial vessel; **ft**, foot; **ftd**, dorsal surface of foot; **int**, anterior loop of intestine; **lpr**, lateral protractor muscle of odontophore; **lt1**, **lt2**, **lt3**, **lt4**, lateral teeth, one to four; **mth**, marginal teeth; **osp**, osphradium; **ov**, ovary; **pen**, penis; **plm**, pallid muscle arising from pallial line; **plt**, pallial tentacle; **plv**, pallial vein; **pog**, posterior oesophageal gland; **pos**, posterior; **rec**, rectum passing through kidney; **rev**, rectum within ventricle; **smu**, shell muscle (scar); **vgp**, vaginal papilla. (**C**, after Hedley 1917; **D**, after Fretter 1984a; **E**, after Beck 1992b) [C. Eadie]

Nerita plicata from Aldabra Atoll in the Indian Ocean, uses landscape clues to locate the sea, detecting either differences in illumination between sea and land or differences in topography (Chelazzi & Vannini 1980). This species is found in the Indo-West Pacific including northern and eastern Australia. When displaced from a resting site by wave action, for example, the Indian Ocean species, *Nerita textilis*, always returns to the exposed rocks. Orientation in *Nerita textilis* is perpendicular to the coast and movement across the rocky shore is usually upwards with a random component (Chelazzi & Vannini 1976). Warburton (1973) suggested that *Nerita plicata*, at least, orientates by the sun, behaving photonegatively in the morning and photopositively in the afternoon. Accuracy improves as the sun's brightness increases; the snails were recorded as orientating away from the sea at all times of the day.

Predation appears to be of minor importance in maintaining population densities (Underwood 1978; Garrity & Levings 1981). Several species of Caribbean *Nerita* exhibit a flight response when approached by sympatric species of Thaidinae (Muricidae) and

Fasciariidae, intertidal gastropods that prey heavily on other molluscs. Escape behaviour includes the elevation of the shell to expose the head, flailing of cephalic tentacles, and increased locomotory activity (Hoffman, Homan, Swanson & Weldon 1978). In an investigation of predation by crabs, Reynolds & Reynolds (1977) compared the robustness of shells of Central American species of *Nerita* from each side of the Isthmus of Panama with species from the West Pacific. They found that the strongest shells occur in the West Pacific populations, coincident with the largest xanthid crabs, and the lightest shells are found in the Western Atlantic where the sympatric xanthids are relatively small. In South Australia, the reef crab *Ozius truncatus* is recorded as preying on small *Nerita atramentosa* lower down on the shore (Chilton & Bull 1984).

Hermit crabs utilise neritid shells. In Senegal, West Africa, the hermit crab *Clibanarius chapini* actively seeks out neritids in preference to other types (Altes 1978). *Nerita scabricosta* is the choice of the terrestrial hermit crab, *Coenobitus compressus* (Abrams 1978).

15. PROSOBRANCHS

Although quite small, neritids are often used as food by humans. Cotton (1959a) reported that shells of *Nerita atramentosa* are common in early Aboriginal middens.

Neritid species are susceptible to onshore pollution. The European brackish-water species *Theodoxus fluviatilis* becomes hyperactive when exposed to low concentrations of crude oil, but its activity is progressively reduced as the concentrations increase, until the animal is completely immobilised (Linden 1977). Nerites are susceptible to both oil and dispersant (Battershill & Bergquist 1982). Following an oil spill off Lamma Island, Hong Kong, the population of *Nerita albicilla* was totally destroyed for thirteen months (Stirling 1977).

Several neritid species are known to be intermediate hosts for trematodes (Chemogorenko, Komarova & Kurandina 1978).

Neritids, usually being shoreline dwellers, are rarely preserved as fossils. However, fossil records of the Neritidae date back to the Triassic (Knight *et al.* 1960b). Little is known of Australian fossils: *Nerita melanotruga* is found in the Early Pliocene of Victoria (T. Darragh personal communication); *Nerita milnesi* was described by Ludbrook (1983) from the Pliocene (probably not Pleistocene as reported) of Kangaroo Island, South Australia; and *Nerita atramentosa* was recorded by Ludbrook (1984) from the Late Pleistocene of South Australia.

Family Phenacolepadidae

The Phenacolepadidae are a small family of shallow-water marine limpets found throughout warmer seas. Two genera with few species are recorded from Australian waters: *Phenacolepas* and *Cinnelepetia*; *Cinnelepetia* is sometimes treated as a subgenus of *Phenacolepas* (Knight *et al.* 1960b). Australian species include *Phenacolepas calva* found in deep water along the southern coast from Tasmania to Western Australia (Cotton 1959a), *P. crenulata* from tropical Queensland to northern Western Australia, *P. immeritus* from north-eastern Queensland, *Cinnelepetia cinnamomea* from the east coast and *C. linguaviverrae* from Torres Strait. Most species are sublittoral, but Hedley (1917) found specimens of *C. cinnamomea* under rocks on mud at Sydney Harbour and the Annam River near Cooktown. *Phenacolepas* species have been found living under deeply embedded rocks, and some species live associated with hydrothermal vents, including some in the Pacific (see Beck 1992b).

The small (less than 10 mm long) shell is patelliform to capuliform, and secondarily bilaterally symmetrical with the apex curved posteriorly (Fig. 15.74A). The shell muscle scar is horseshoe-shaped and opens anteriorly (Fig. 15.74B). The apical whorls of the shell are typically helicoid, but the characteristic limpet shape is produced by a disproportionate expansion of the last whorl. There is a sculpture of radiating ridges and lines overlain by a periostracum. A fully developed operculum is lacking, although a vestigial one is enclosed by the tissue of the foot. This rudimentary operculum has remnants of apophyses and is attached to part of the left and right columellar muscles (Fretter 1984a).

Fretter (1984a) recorded that the Persian Gulf species, *Phenacolepas omanensis*, is active, responding immediately to disturbance. The sole of the foot is ciliated, and its margin is cuticularised. When at rest, the middle part of the sole is raised slightly to form a shallow cavity while the edge of the foot remains in contact with the substratum. The differential in pressure created by this action pushes down on the shell and keeps the animal securely in place. The pedal musculature of *Phenacolepas* is less well developed than that of true limpets (Patellidae, Acmaeidae), and this may be related to the much more sheltered habitat that *Phenacolepas* species occupy.

The external and internal features of phenacolepids are illustrated in Figure 15.74C and 15.74D respectively. The long cephalic tentacles have eyes at their bases, and the foot is ovate. The mantle is fringed with contractile papillae and a broad band of

antiseptic or repugnatorial glands. The mouth is encircled by an oral veil and a band of subepithelial glands. The radula has a large, flat, square central tooth, four lateral teeth, and numerous marginals (Fig. 15.74E). The fourth lateral has an axe-shaped cusp which mines the substratum for food, principally for detritus.

The right auricle is lost, and the Phenacolepadidae are unique among the neritoideans in having erythrocytes in the blood. These red blood cells are biconcave discs about 25 µm in diameter (Fretter 1984a). The pleural ganglia and pedal cords are fused, as are the supra- and suboesophageal ganglia. The supra-oesophageal connective is lost.

The female bears a grooved vaginal papilla which may be analogous to an ovipositor (Fig. 15.74D). The male has a digitiform penis associated with the right tentacle (Fig. 15.74C). There is no connection between the vas deferens and the penis; sperm are conducted along a groove in the body wall (Fretter 1984a). The bursa copulatrix can accommodate a large quantity of sperm, and Fretter (1984a) recorded up to ten club-shaped spermatophores occupying a single bursa.

Fossil records of the Phenacolepadidae extend back to the Eocene (Knight *et al.* 1960b). In Australia, few fossils have been recorded. Ludbrook (1941) recorded *Phenacolepas tela* from the Dry Creek Sands Formation of South Australia; this formation is probably Late Miocene and not Pliocene as previously thought (T. Darragh personal communication).

Family Titiscaniidae

The family Titiscaniidae comprises a single species, *Titiscania limacina* (Fig. 15.75A). The animal is small, shell-less and slug-like, superficially resembling an opisthobranch. Discovered in the Philippines, *Titiscania limacina* was illustrated and named by Bergh in 1875. In 1890 he published a description based on

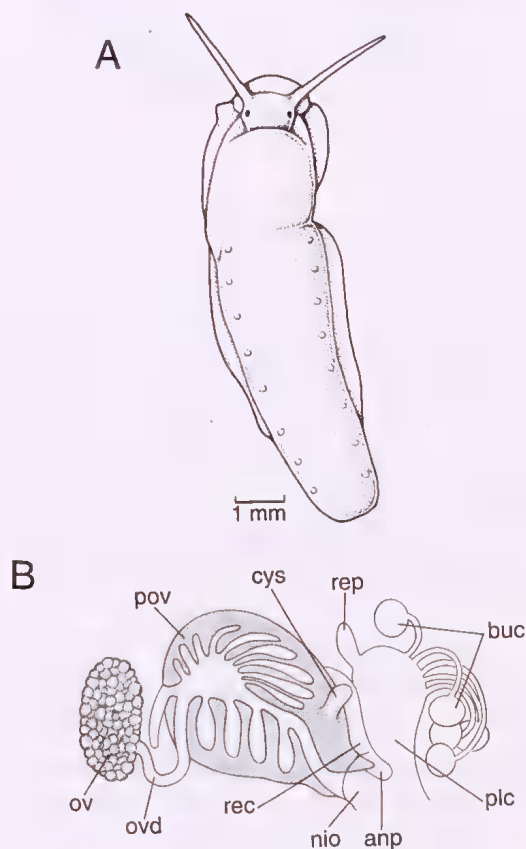


Figure 15.75 Family Titiscaniidae. *Titiscania limacina*: A, dorsal view of animal; B, female reproductive system. anp, anal papilla; buc, bursae copulatrix; cys, crystal sac; nio, nidamental opening; ov, ovary; ovd, oviduct; plc, pallial cavity; pov, pallial oviduct; rec, rectum; rep, renal opening. (A, B, after Marcus, Ev. & Marcus, Er. 1967) [A, B. Scott; B, D. Wahl]

further specimens from Mauritius. *Titiscania limacina* is marine, living in shallow waters on coral reefs. Australian records are from Michaelmas Cay near Cairns and Broadhurst Reef off Townsville (Burn 1975). It has also been recorded from Eniwetok, the Pacific coast of Panama, and the Gulf of California (Marcus, Ev. & Marcus, Er. 1967).

The animal is dorso-ventrally flattened and elongate. It is yellow or white in colour with a row of twelve paler papillae along each side, and has long cephalic tentacles. The papillae mark the outlets of defensive glands that discharge white threads when the animal is disturbed (Bergh 1890; Marcus, Ev. & Marcus, Er. 1967).

The central and inner two lateral teeth of the radula are absent; the remaining laterals increase in size towards the large fifth lateral. There are more than a hundred marginal teeth in each row (Marcus, Ev. & Marcus, Er. 1967).

The heart has two auricles, and the intestine opens at a papillate anus. The mantle cavity lies close to the head, and has only a narrow anterior opening. The ctenidium is bipectinate, with up to forty lamellae, and may project partially from the opening of the mantle cavity.

The female has a short oviduct, mucous glands, a capsule gland and a seminal receptacle; the bursa copulatrix has numerous ovoid bodies connected to the mantle cavity by ducts (Fig. 15.75B). The male has a long, coiled vas deferens which leads to a minute penis pit behind the right eye.

The Titiscaniidae remains a poorly known group with few specimens available for study.

Family Hydrocenidae

The Hydrocenidae are an exclusively terrestrial group, widespread in the warmer parts of the Old World, Polynesia (Solem 1988) and Hawaii (Pilsbry 1928). Five species in one genus, *Georissa*, are known from mainland Australia (Solem 1988; Smith 1992). *Georissa multilirata* is found in north-eastern Queensland, and *G. minuta* is confined to the karst limestone of the Chillagoe region, near Cairns. The limestone outcrops around Rockhampton support *G. postulata*. *Georissa laseroni*, found in north-eastern New South Wales, is the southernmost species. The single Western Australia species, *G. obesa*, is known only from the Ningbing Ranges and Jeremiah Hills near the Northern Territory border. Outside mainland Australia, *Monterissa gowerensis* is restricted to woodland on Lord Howe Island (Iredale 1944; Smith 1992).

The shells are usually small (less than 10 mm), conical to globose, with few whorls (Fig. 15.76A). The inner whorls are resorbed as the shell grows, so the adult shell is poorly calcified. The lip is simple and neither flared nor reflected, making it difficult to determine whether a shell is adult or subadult. The semicircular operculum is calcareous and has a digitiform apophysis (Fig. 15.76B, C).

Hydrocenids lack true tentacles, but sometimes have broad tentacular processes on the sides of the head. The eyes, raised on papillae, are large (Thiele 1910). The central and lateral teeth of the radula are thin and loosely attached to the radular membrane (Fig. 15.76E); the marginal teeth are numerous (Fig. 15.76D; Climo 1973). Little is known of their diet, but the calcicolous Malayan species *Hydrocena monerosatiana* feeds on algae, moss and lichen (Berry 1961).

There is a single left auricle and a ventricle. The left kidney has a tubular urinary chamber, the right kidney is absent. No longer required for underwater respiration, the ctenidium has degenerated and the highly-vascularised mantle cavity has taken over the role of a lung (Thiele 1910).

Hydrocenids are dioecious and monaulic. The males lack a penis, but the females have a seminal receptacle (Thiele 1910).

Fossil records of the Hydrocenidae extend back to the Pleistocene (Knight *et al.* 1960b).

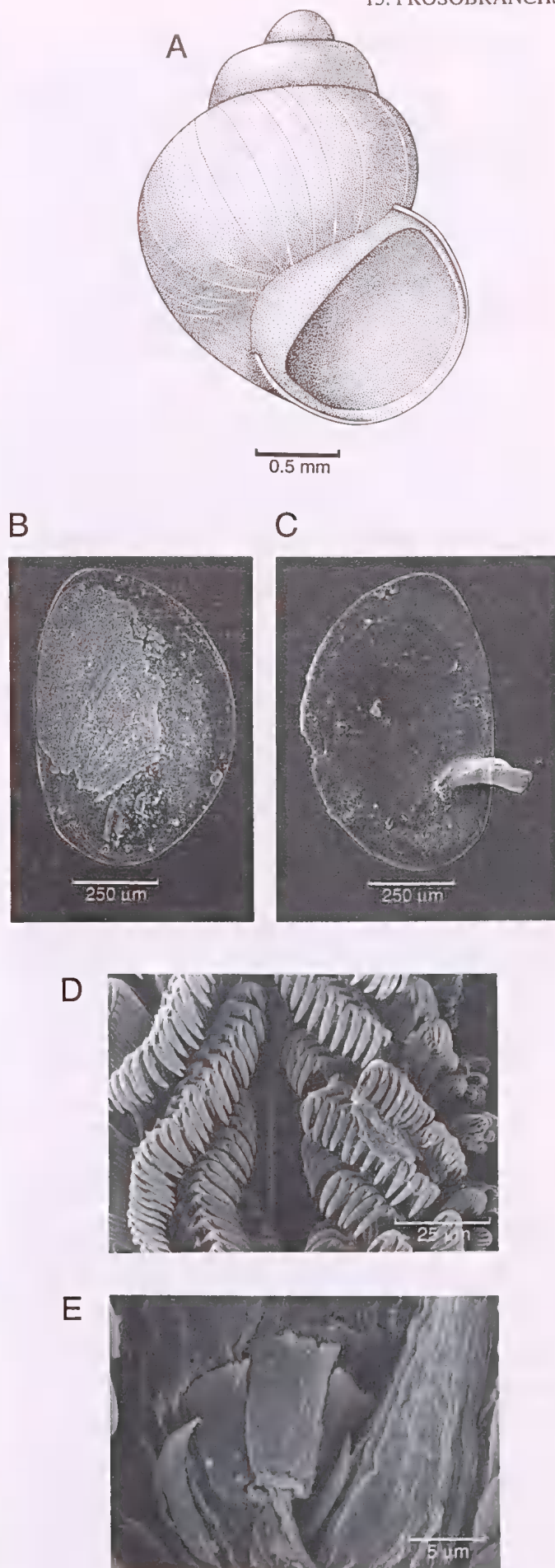


Figure 15.76 Family Hydrocenidae. A, *Monterissa gowerensis*, shell, apertural view. B–E, *Georissa laseroni*: B, operculum, outer surface; C, operculum, inner surface; D, several transverse radular rows, showing the reduced central and inner lateral teeth, the outer laterals, and the conspicuous marginal teeth; E, details of the reduced central and inner lateral teeth.

[A, C. Eadie; B–E, Queensland Museum]

Family Helicinidae

Helicinidae are a family of small- to medium-sized terrestrial, air-breathing neritoideans. They are found in Central and South America, the Caribbean islands, South-East Asia, New Guinea, northern and eastern Australia, Polynesia and parts of Micronesia (see Benthem Jutting 1948; Solem 1959, 1988). Several groups within the family are thought by some workers to warrant subfamilial status, but others have split the family into three: Helicininae, Ceresinae and Proserpininae (Thompson 1980). In this treatment a single family, Helicinidae, with a number of subfamilies, including Helicininae, Ceresinae and Proserpininae, is recognised. At least six species occur in Australia, all belonging to the genus *Pleuropoma* in the subfamily Helicininae. Most of these are arboreal, but some such as *P. macleayi* from Chillagoe, North Queensland, are terrestrial and markedly calcicolous. *Pleuropoma gouldiana* is also found in North Queensland, from Cooktown to the Torres Strait Islands. Two other species have large distributions in eastern Queensland: *P. draytonensis* and *P. gladstonensis*. The southernmost species, *P. jana*, occurs in New South Wales, where it may be thermally limited (Bishop 1980). One species, *P. walkeri*, appears to be widely distributed across the north of the continent from north-western Australia to the Gove Peninsula (Smith 1992).

Shells may be conical, globose to flattened, with a semicircular aperture (Fig. 15.77A). The operculum (Fig. 15.77B), when present, is composed of two layers, the inner corneous and outer calcareous. A true apophysis is lacking, but there is usually a small ridge for muscle attachment. In the subfamilies Proserpininae and Proserpinellinae, the operculum has been lost and the aperture is armed with numerous folds and teeth that function to reduce water loss and prevent predation by similar-sized enemies. The Helicinidae are the only group of terrestrial snails other than some pulmonates with these apertural barriers (Bishop 1980).

In Helicininae and Ceresinae, the large foot has a shallow pedal groove close to the foot margin, whereas in the Proserpininae the foot has a deep pedal groove which lies well above the foot margin. The tentacles are long, and the eyes are situated at their bases. The rhipidoglossate radula is rather complex, with the first three lateral teeth extremely variable; the fourth functions as the rasping tooth (Fig. 15.77C, D; Bourne 1911; Baker 1922).

The heart has either two nearly equal-sized auricles (Ceresinae) or a single left auricle (Helicininae, Proserpininae) (Thompson 1980).

Helicinids are dioecious. Fertilisation is internal and involves the transfer of a spermatophore. The males lack a penis, but have a convoluted vas deferens, a prostate gland, and a distal sac. The prostate is simple in the Ceresinae, but is divided into two parts in the Helicininae and the Proserpininae. Females are diallic or triaulic, with one tract opening into the mantle cavity to receive spermatophores, and another near the anus for egg deposition. In the Helicininae, the vagina opens into the hypobranchial duct. The female reproductive system is complex, and has a seminal receptacle, bursa copulatrix, egg gland and accessory sperm sac (Bourne 1911; Baker 1925; Thompson 1980).

Most helicinids are terrestrial, inhabiting leaf litter in moist forest; some are tree-dwelling. Helicinids are generally too small to be of economic importance. However, records exist of the American species, *Helicina orbiculata*, causing damage in citrus orchards by feeding on the fruit, and thus allowing the invasion of destructive rot fungus and frugivorous beetles (Dundee & Cancienne 1978).

The earliest record of the Helicinidae may be from the Carboniferous of North America (Simroth 1910; Solem & Yochelson 1979), but the next oldest record is from the Upper Cretaceous of Europe (Knight *et al.* 1960b) and North America (Bishop 1980).

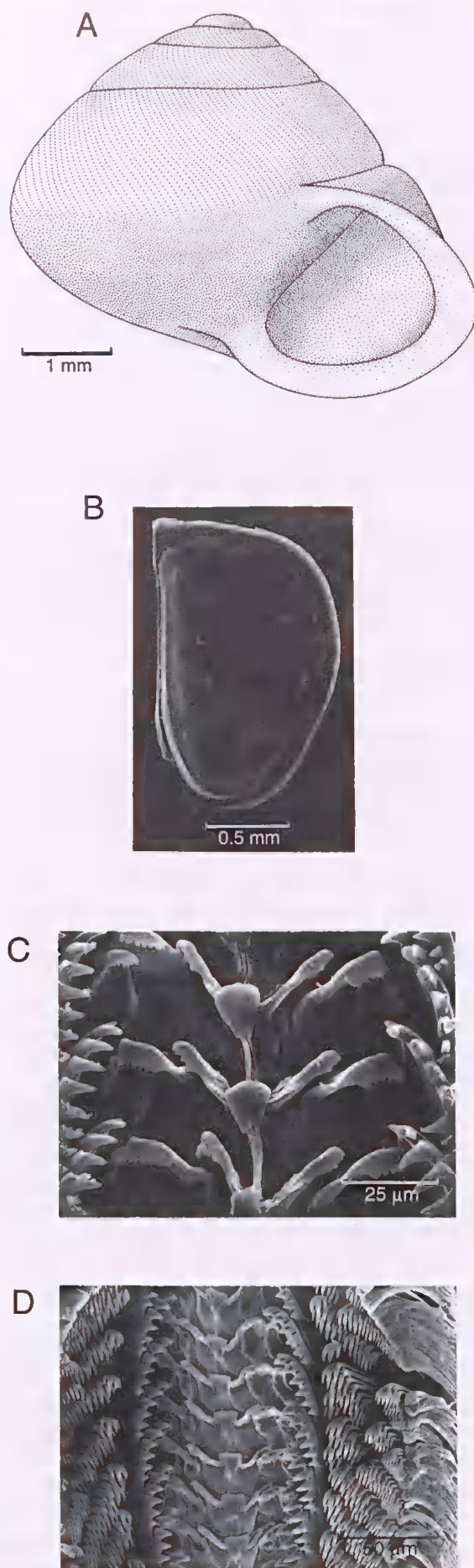


Figure 15.77 Family Helicinidae. A, *Pleuropoma draytonensis*, shell, apertural view. B, *Pleuropoma jana*, operculum, outer surface. C, D, several transverse rows of radula, showing details of central, lateral and marginal teeth: C, *Pleuropoma draytonensis*; D, *Pleuropoma jana*.

[A, C. Eadie; B–D, Queensland Museum]

APOGASTROPODA

The Apogastropoda comprises the two groups, Caenogastropoda and Heterobranchia. This grouping is defined by a number of reductionist characters, probably the result of (possibly independent) heterochronic processes, and possible convergent characters such as the epiathroid nervous system and planktotrophic larva (Ponder 1991a). There are, however, also several synapomorphic eusperm characters that appear to support a common ancestry (Healy 1993a). Healy (1993a) also listed several apomorphic characters for caenogastropod sperm and several for heterobranch sperm.

Developmental data are also cited by Haszprunar (1993) as indicating a common origin for caenogastropods and heterobranchs, notably the accelerated formation of the mesentoblast and prototroch. However, acceleration of the mesentoblast involves different mechanisms in heterobranchs and caenogastropods (Freeman & Lundelius 1992; Ponder & Lindberg 1997). The acceleration of the prototroch in Caenogastropoda and Heterobranchia may also be a convergent phenomenon and related to the generally accelerated development in both of these groups.

Superorder CAENOGASTROPODA

The Caenogastropoda encompasses several major groups, the Architaenioglossa (Cyclophoroidea, Ampullarioidea), Neotaenioglossa (*sensu* Haszprunar 1985a and Ponder & Warén 1988), Ptenoglossa and Neogastropoda, although, monophyly of some of these groups is doubtful as their relationships are still not well resolved (Ponder & Warén 1988; Ponder & Lindberg 1997). These groups are briefly discussed below.

The Architaenioglossa contains two non-marine groups, the Cyclophoroidea and Ampullarioidea. They form a rather poorly supported clade which may prove to be paraphyletic (Haszprunar 1988a). They are regarded as 'archaeogastropods' by Haszprunar (1988a), but are included in the Caenogastropoda or an equivalent group by most other workers (for example, Thiele 1929–1935; Wenz 1938–1944; Taylor, D.W. & Sohl 1962; Ponder & Warén 1988; Ponder & Lindberg 1996, 1997). Architaenioglossans differ from all other caenogastropods in having a hypoathroid or partially hypoathroid nervous system and lacking Si cells in the osphradium.

Ponder & Lindberg's (1996, 1997) analyses show that Architaenioglossa is the sister group to the remainder of the caenogastropods, a clade they called Sorbeoconcha (Ponder & Lindberg 1997), comprising Cerithioidea, Campaniloidea, Ptenoglossa, and the rest of the caenogastropods, including Neogastropoda. The Sorbeoconcha is characterised by having the flow of water into the mantle cavity under inhalant control, not exhalant as in nearly all other gastropods (Lindberg & Ponder in preparation), an epiathroid nervous system, Si cells in the osphradium and several other features. Thus, this clade includes many of Thiele's (1925a, 1929–1935) Mesogastropoda, as well as the Neogastropoda.

Neotaenioglossa (used by Haszprunar 1985a and Ponder & Warén 1988 as a substitute for Mesogastropoda) is a paraphyletic grade. Calyptraeiformii, as used by Golikov & Starobogatov (1988), is equivalent to Neotaenioglossa. This grade comprises several large clades, the sister to the rest being the Cerithioidea, as advocated by Fretter (1980). Cerithioideans share sperm characters with architaenioglossans (Healy 1988a), lack a penis and typically have spermatophores and open pallial genital ducts. The families within the Cerithioidea have been subjected to phylogenetic analyses by Houbbrick (1988) and Ponder (1991b).

The Campaniloidea is related to cerithioideans, but is sufficiently distinct to be regarded as a separate superfamily (Houbbrick 1981a, 1989; Haszprunar 1985b, 1988a, 1992b; Healy 1986b). Haszprunar (1985d, 1988a) regarded *Campanile* as the sister group to heterobranchs, but this idea was rejected by Ponder &

Warén (1988), Houbbrick (1989) and Ponder & Lindberg (1996, 1997) and is not supported by sperm (Healy 1986b) or osphradial (Haszprunar 1992b) ultrastructure.

The taxa considered to be the 'higher caenogastropods' (Healy 1988a), the Hypsogastropoda of Ponder & Lindberg (1997), form another clade that includes the Neogastropoda and the members of the paraphyletic Neotaenioglossa, excluding Cerithioidea and Campaniloidea. Synapomorphies for these groups include filiform paraspermatozoa, characteristic euspermatozoa (Healy 1988a) and the development of a penis.

The Ptenoglossa (= Ctenoglossa) is almost certainly paraphyletic or polyphyletic and includes the Triphoroidea, Janthinoidea and, possibly, Eulimoidea. They share some features with cerithioideans and the higher neotaenioglossans.

The taenioglossate 'higher caenogastropods' can be referred to as Littorinimorpha, a name used by Golikov & Starobogatov (1975) for essentially the same grouping and redefined by Ponder & Lindberg (1997). It includes, in large part, the group called Neomesogastropoda by Bandel (1993b) and Bandel & Riedel (1994). This group may be paraphyletic, depending on the identification of the sister group of Neogastropoda (see below). It is in part equivalent to the paraphyletic Mesogastropoda of Thiele (1929–1935) and Neotaenioglossa and Discopoda + Heteropoda of Ponder & Warén (1988) but, as used here, excludes the Cerithioidea, Ptenoglossa, and Campaniloidea.

Heteropoda is usually used as a higher grouping (see for example, Ponder & Warén 1988). However, this highly modified pelagic group may have as its sister group the Vanikoridae or Pickworthiidae (Bandel & Hemleben 1987; Bandel 1993a). Consequently, heteropods can be considered as being contained within the Littorinimorpha, and, despite their highly derived morphology and habits, do not require separate recognition at the same level as the other groups discussed here. In this volume we simply recognise the superfamily Carinariioidea and use the term heteropod informally.

The Neogastropoda (or Stenoglossa) is a large and probably monophyletic group of mainly carnivorous gastropods comprising the superfamilies Muricoidea, Cancellarioidea and Conoidea (= Toxoglossa). They are grouped on the basis of several synapomorphies (Ponder 1973a) and are discussed in more detail below in the treatment of Neogastropoda and the relevant superfamilies.

Order ARCHITAENIOGLOSSA

Superfamily CYCLOPHOROIDEA

Cyclophoroideans are operculate, ground-dwelling and arboreal land snails with very small to large, discoidal, turbinat, turreted or pupiform shells. The shells are smooth or spirally or radially ribbed, and with or without characteristic markings. The aperture is usually circular, sometimes with tubercles, folds, breathing canals or tubes. The operculum is corneous or calcareous, mostly multispiral.

The radula is taenioglossate. There is no ctenidium or gill of any kind and the mantle cavity is developed into a thin vascularised sac (lung). There is no osphradium, but the hypobranchial gland is sometimes present. Cyclophoroideans are dioecious, and some species are ovoviviparous. The male and female pallial gonoducts either have a small terminal opening or are broadly open ventrally. The female reproductive system has a well-defined pallial oviduct, a seminal receptacle and a bursa copulatrix. Males may or may not have a tapering penis situated below the right tentacle (Tielecke 1940; Benthem Jutting 1948). Tielecke (1940) provided a comprehensive phylogenetic analysis of the cyclophoroidean families. Solem (1959) recognised five families – the Poteriidae, Maizaniidae, Cyclophoridae, Pupinidae and Diplommatinidae (= Cochlostomatidae). The latter three families occur in Australia.

Family Cyclophoridae

Cyclophorids are very small to large (5–40 mm in height, and up to 60 mm in width) terrestrial snails with dextral or sinistral, discoidal to turbanate shells which occasionally may be loosely coiled (Fig. 15.78A). The aperture is either circular or subcircular with a thickened or reflected lip, and the operculum is horny or calcareous, and multispiral (Fig. 15.78B). Some species have elaborate colour patterns or periostracal extensions, but these are lacking in Australian species. This diverse family has a tropical distribution throughout South-East Asia, the Philippines, India, Madagascar and Africa, with a few species reaching the western Pacific and northern Australia.

Kobelt (1902) was the first to revise the world Cyclophoridae, but no major review of the Australian taxa has been completed. J.C. Cox (1907) provided a checklist of Australian species based on Kobelt's classification, and Iredale (1937a) listed the species without making critical comment. Burch (1976) listed three species belonging to two genera. Solem (1988) added a new species of *Leptopoma* from the Northern Territory. Smith (1992) listed two genera containing four species. The genus name *Ditropisena*, proposed by Iredale (1933), was used as a subgenus of *Ditropis* and included the two Australian endemic species. *Ditropisena*, however, is now included in the Assimineidae (Fukuda in preparation). In the Australian fauna, *Ditropis* now includes two endemic species – *D. macleayi* and *D. whitei*, from northern Queensland. These have a small, discoidal shell with several keels, and a subquadrate aperture and are poorly known; they occur under timber on the ground.

Australian cyclophorids have small, dextral shells. The two remaining species in Australia belong to the genus *Leptopoma*. Species of *Leptopoma* have white, turbanate shells with a strongly reflected lip and a spirally lirated protoconch (Fig. 15.78A). The operculum is generally multispiral (Fig. 15.78B). *Leptopoma minus* occurs in the Northern Territory and ranges to Indonesia and *L. perlucida*, occurs from coastal tropical Queensland through New Guinea to the Philippines. Details of life history and behaviour of the Australian species are unknown. *Leptopoma perlucida* is always found on the leaves of trees.

Cyclophorids have slender cylindrical tentacles with the eyes on their outer bases, usually on short peduncles. The mantle cavity is a vascularised pulmonary sac. The central tooth of the radula has a large central cusp with two to four lateral cusps (Fig. 15.78C). The lateral and marginal teeth have two to four cusps. Females have a seminal receptacle and bursa copulatrix; the two structures are separate (Fig. 15.78D). Males have an open pallial sperm groove and conoidal penis. Some anatomical data on the Australian species are given by Jonges (1980). He also reviewed the genital anatomy of some extralimital species of *Leptopoma* and provided a summary of some earlier anatomical studies (see also Kretzschmar 1919; Schneider 1920; Tielecke 1940; Morton, J.E. 1952; Berry 1964b; Thompson 1969; Kasinathan 1975; Girardi 1978). Andrews & Little (1972, 1982) provided details of kidney function and physiology in a number of cyclophorids, among them *Leptopoma perlucida*.

Cyclophorids appear to be recent immigrants from the Indo-Malayan region. Presumably they managed to colonise Australia following the Miocene collision of the Australian and Asian plates (Bishop 1981). The Australian species of *Leptopoma* also occur in Indonesia and the Philippines where the genus is more diverse. The fact that cyclophorids have not colonised the subtropics as successfully as have the Pupinidae and Diplommatinidae suggests that they entered Australia after the creation of the dry corridors north of Rockhampton and north of Bowen (Dick 1964). Important reviews of cyclophorid taxonomy in the Indo-Pacific region include those of Benthem Jutting (1948), Clench (1949), Solem (1959) and Girardi (1978).

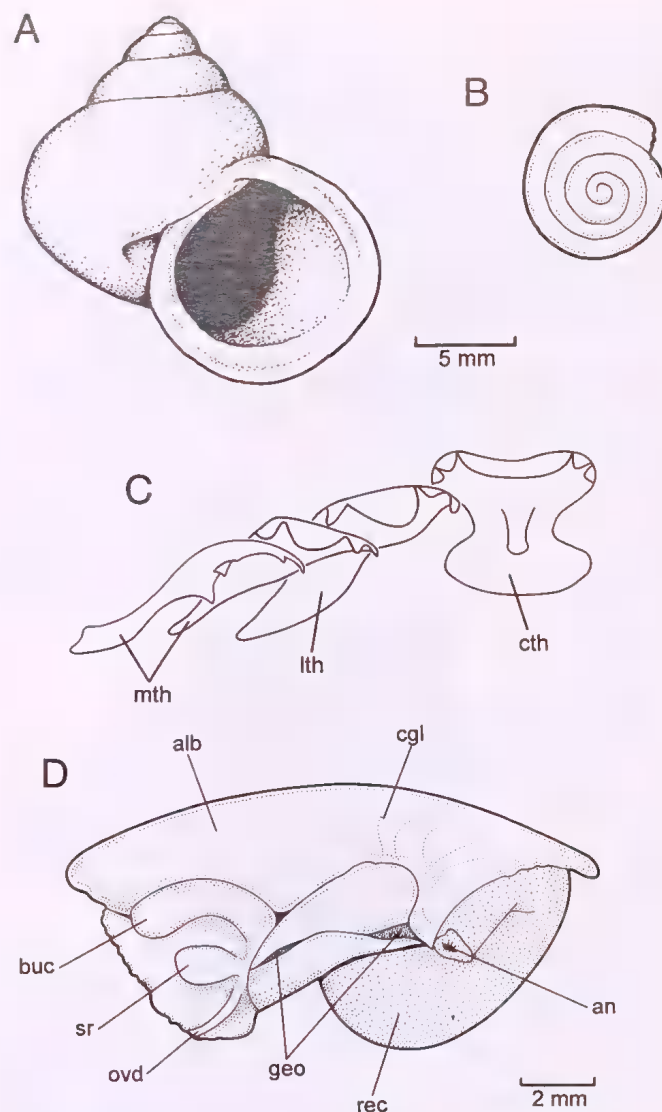


Figure 15.78 Family Cyclophoridae. A, B, *Leptopoma perlucida* from northern Queensland: A, shell, apertural view; B, operculum, outer surface. C, *Leptopoma vitreum* from Malaysia, half a transverse row of the radula. D, *Leptopoma perlucida*, female genital tract, left lateral view. alb, albumen gland; an, anus; buc, bursa copulatrix; cgl, capsule gland; cth, central tooth; geo, genital opening; lth, lateral tooth; mth, marginal teeth; ovd, oviduct; rec, rectum; sr, seminal receptacle. (C, after Benthem Jutting 1948; D, after Jonges 1980) [A, B, B. Scott; C, C. Eadie; D, D. Wahl]

Family Pupinidae

Members of this family are small to large (5–50 mm shell length) terrestrial snails with moderately to strongly elevated pupiform shells which vary in colour from white to yellow, occasionally with a pinkish to reddish hue. The shells may be smooth and glassy or dull with prominent axial sculpture (Fig. 15.79A–D). The external appearance of these snails is illustrated in Figure 15.79F.

The first Australian species were described very early in the second half of the 19th Century. An early listing of species was provided by J.C. Cox (1868). Members of this group were placed in the subfamily Pupininae within the family Cyclophoridae. Kobelt, in 1902, completed the first major review of worldwide cyclophorid taxa, and shortly afterwards J.C. Cox (1907) published a more up-to-date list of species from Australia and adjacent islands, using Kobelt's classification. Tielecke (1940) presented a review of higher taxonomic categories based on details of the nervous system, genitalia and pallial structures. His familial division of the cyclophoroidean groups, including the elevation of Pupinidae to familial status, has been adopted by subsequent authors (Wenz 1938–1944; Solem 1959; 1978; Golikov & Starabogatov 1975). Two subfamilies are recognised

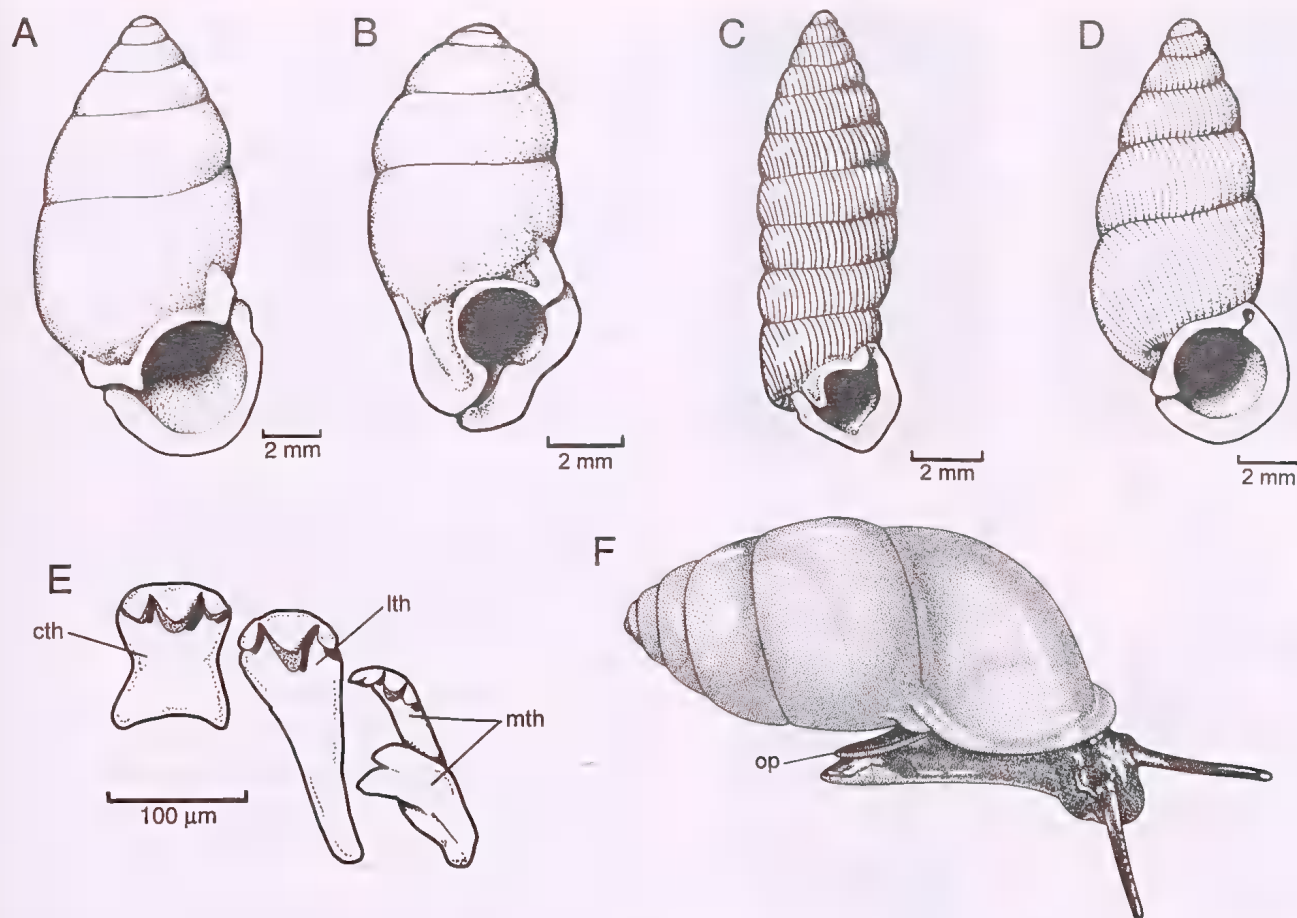


Figure 15.79 Family Pupinidae. A–D, shells, apertural view: A, *Pupina (Signepupina) meridionalis*, from mid-eastern Queensland; B, *Pupina (Signepupina) thomsoni*, from North Queensland; C, *Hedleya macleayi*, from North Queensland; D, *Pupinella (Necopupina) planilabris*, from mid-eastern Queensland. E, *Pupina (Signepupina) thomsoni* from northern Queensland, half of a transverse row of the radula. F, *Pupina (Signepupina) coxeni* from south-eastern Queensland, external appearance of crawling animal. cth, central tooth; lth, lateral tooth; mth, marginal teeth; op, operculum. (E, after Beddome 1897; F, after photograph by Queensland Museum)

[A–E, B. Scott; F, C. Eadie]

presently within the Pupinidae (see Tielecke 1940) – the Pupininae and Pupinellinae, and it is probable that both are represented in Australia. Iredale (1937a) created several ‘genera’ for the Australian species, but Solem (1959) considered them to be only of sectional or subgeneric value.

Australian species have shells which are usually solid, less than 15 mm in length, dextral, with a thickened, sometimes duplicated lip which may or may not have one or two breathing canals (Fig. 15.79A–D). Shells of species of *Pupina (Signepupina)* (Fig. 15.79A, B), *Hedleya* (Fig. 15.79C) and *Pupinella (Necopupina)* (Fig. 15.79D) are representative of the various pupinid shell forms that occur. The operculum is horny and multispiral. Anatomical data on the Australian species are lacking, but the two subfamilies are readily separated by differences in their anatomy (Tielecke 1940). In the Pupininae, the seminal receptacle is a process of the bursa copulatrix, whereas the Pupinellinae have the normal condition of the seminal receptacle separate from the bursa copulatrix and connected directly to the oviduct. Pupinids have separate sexes and males may or may not have a penis. Beddome (1897) presented details of the jaw and radula of *Pupina thomsoni* (= *P. bidentata*) (Fig. 15.79E). The life cycles of the Australian species are unknown.

Members of the family in Australia are confined to closed forests. They occur coastally from the humid, wet tropical mesophyll vine forests of northern Queensland to the warm subtropical rainforests of northern New South Wales, and the drier subtropical vine forests and thickets of south-eastern Queensland. They are terrestrial and are usually found in moist litter under logs, or in accumulated litter and debris among rock strewn substrata. Individual species have small geographic ranges and several may occur sympatrically.

The family contains numerous genera that occur from South-East Asia through Melanesia, Micronesia, Papua New Guinea and Australia. Iredale (1937a) listed eight genera and two subgenera for Australia, although their status has yet to be thoroughly investigated. Burch (1976) listed 25 species and one subspecies, and Smith (1992) listed four genera – *Hedleya*, *Pupina*, *Pupinella* and *Suavocallia* – with 19 endemic species. However, recent fieldwork in northern Queensland indicates that there are still a number of additional species to be described. There is no fossil record of the family in Australia.

Family Diplommatinidae

Diplommatinids are very small (less than 10 mm in length) terrestrial land snails which usually have either a sinistral (*Diplommatina*) or dextral (*Vealepalaina*), high-spined, ovately conical shell in which the last whorl may be constricted or somewhat inflated (Fig. 15.80A–D). In *Diplommatina*, the penultimate whorl forms the widest point of the shell. The lip is strongly reflected (especially in *Vealepalaina*), and the operculum is horny and multispiral. Small folds or denticles are present in the aperture of some species. Strong axial ribs are characteristic.

Two subfamilies are recognised – the Cochlostomatinae and the Diplommatininae. The former includes species from montane regions of eastern Europe whereas the latter includes species found in South-East Asia, Micronesia, Melanesia and Australia. Solem (1959) discussed generic groupings within the Diplommatininae and provided a useful compilation of literature sources. Tillier (1981) reviewed the status of the New Caledonian diplommatinids in a study which examined the problem of geographic variation in shell features. In another recent study, Vermeulen (1993) reviewed a major radiation of *Diplommatina* in Borneo.

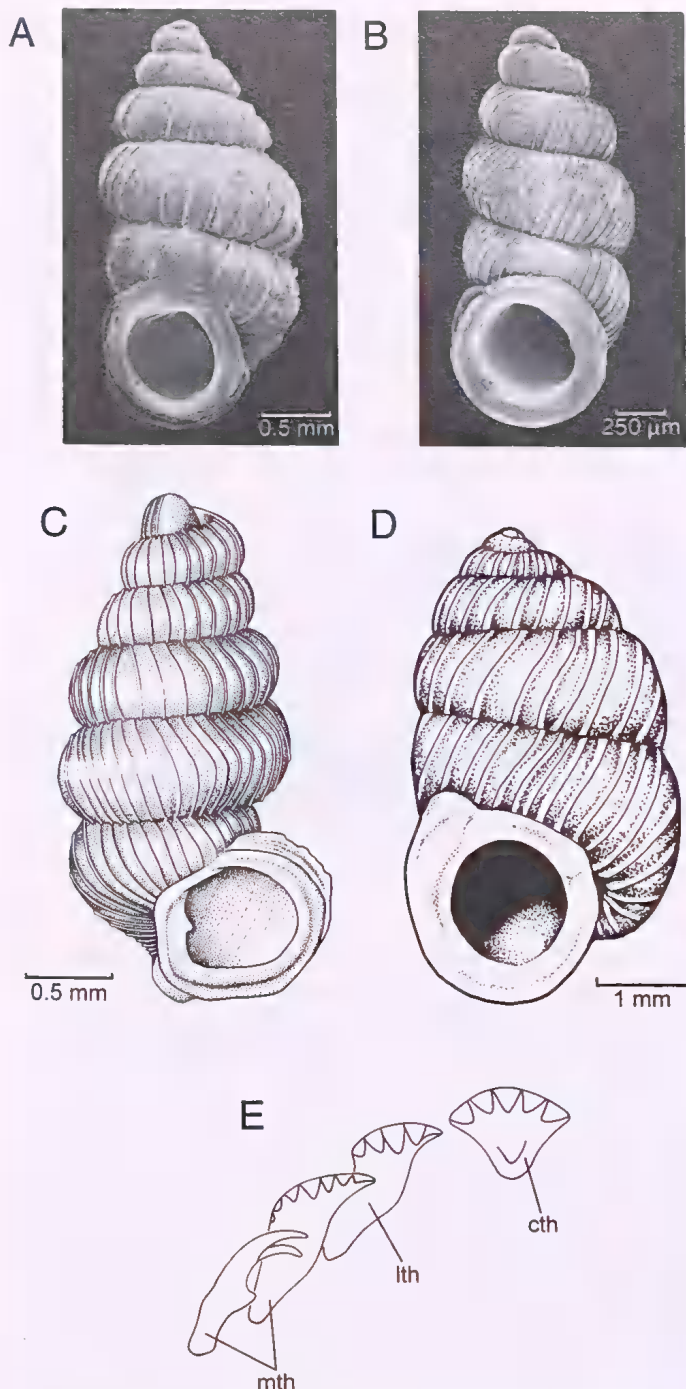


Figure 15.80 Family Diplommatinidae. A–D, shells, apertural view: A, *Velepallaina strangei* from south-eastern Queensland; B, *Velepallaina beddomei* from northern Queensland; C, *Diplommatina (Eclogarinia) gowllandi*, from northern Queensland. D, *Palaina macgillivrayi* from Lord Howe Island. E, *Diplommatina sulcicollis* from Java, half a transverse row of the radula. cth, central tooth; lth, lateral tooth; mth, marginal teeth. (E, after Benthem Jutting 1948)

[A, B, Queensland Museum; C, A.J. Hill; D, B. Scott; E, C. Eadie]

Australian species are poorly known. Three mainland endemic species were recorded by Iredale (1937a) and listed by Smith (1992) – *Velepallaina strangei* from northern New South Wales and southern Queensland (Fig. 15.80A); *Velepallaina beddomei* from northern Queensland (Fig. 15.80B); and *Diplommatina (Eclogarinia) gowllandi* from Fitzroy Island, northern Queensland (Fig. 15.80C). The presence of an apertural denticle on the parietal wall of *Diplommatina (Eclogarinia)* species readily separates them from *Velepallaina* species. The detailed distributions of these species have yet to be determined and although they bear strong similarities in shell features to nearby Asian and Pacific taxa, the lack of anatomical data prevents accurate determination of their affinities. Iredale (1933, 1937a) erected separate generic units for the Australian species. An extensive radiation of diplommatinids has occurred on Lord Howe Island, and several species also occur

on Norfolk Island (Iredale 1944, 1945). Smith (1992) listed the genera *Fermepallaina* (2 species) and *Palmatina* from Norfolk Island, and one genus, *Palaina*, with 10 species and four subspecies from Lord Howe Island (Fig. 15.80D).

Sexes are separate and males may or may not have a penis. The radula is taenioglossate. Benthem Jutting (1948) presented data on the radulae of Indo-Malayan species and showed that the central tooth has five to seven cusps, and the lateral and marginal teeth have three to five cusps (Fig. 15.80E).

Specimens of *Velepallaina strangei* and *V. beddomei* have been collected from leaf litter among volcanic talus in rainforest; the animals were white in colour. *Diplommatina (Eclogarinia) gowllandi* has been taken in similar situations on Fitzroy Island. The Lord Howe Island and Norfolk Island taxa are also primarily litter species.

Although the first Australian species were recorded in the middle of the 19th Century very little information has been obtained subsequently and few collections made. The combination of small size and relatively specialised habitat has contributed to the fact that very few specimens of the mainland species are currently available for study. It is highly probable that further species will be discovered.

Superfamily AMPULLARIOIDEA

Ampullarioideans are operculate freshwater snails with very small to large shells (10–150 mm in length and up to 150 mm in diameter) which are ovately conic, globosely turbinata, or rarely, pyramidal or planorbiform. Shell sculpture is either absent or present as axial ribs, spiral cords, nodules and malleations. Shell colour varies from brown to green, and greenish-yellow with, or without, darker spiral bands and blotches. The operculum is corneous or calcareous, concentric or paucispiral, with a central or excentric nucleus (Benthem Jutting 1956).

The radula is taenioglossate. A monopectinate ctenidium is present in the mantle cavity and members of the family Ampullariidae also have an apomorphic separate lung. Ampullarioidean animals feed largely by ciliary methods. An osphradium is present. Members of both families have an exhalant siphon; ampullariids also have an inhalant siphon. Sexes are separate, and females may be oviparous or ovoviviparous. Males may have either a primary verge or a secondarily modified intromittent organ.

Two families are recognised: the tropical Ampullariidae (= Pilidae) and the widespread Viviparidae. The family Viviparidae is native to Australia, but introduced species of both families have become available through the aquarium trade.

Family Viviparidae

Viviparids are freshwater snails, with medium to large-sized (up to 150 mm in length, the Australian species up to 40 mm in length), ovately conic to globosely turbinata shells (Fig. 15.81A–C). The colour of the shell varies from greenish-brown to brown and yellow, often with darker spiral bands. The adult whorls are strongly convex and the aperture is generally large, circular to subcircular, with a simple, unreflected lip. The operculum is corneous with a subcentral nucleus and concentric growth rings. Shell sculpture is usually absent but may consist of spiral lines, ridges and tubercles in some species. The protoconch may have a combination of fine spiral ridges and periostracal hairs.

Three subfamilies are recognised – the Viviparinae from Europe, Asia and North America; the Campelominae from North America; and the Bellamyinae from South-East Asia, Japan and Australia.

Cotton (1935a) presented a brief review of the Australian species and introduced *Notopala* (type species: *Paludina hanleyi*) and *Centrapala* (type species: *Paludina lirata*) for the conically turbinata species. Iredale (1943) further subdivided *Notopala* on the basis of findings by Prashad (1928). Stoddart (1982) rejected

Iredale's classification (which was based solely on conchological detail) and provided synonymies of the western Australian species. A different shell form occurs in *Larina* (type species: *L. strangei*) which has the apical whorls greatly reduced in size and number, and the last whorl greatly inflated (Fig. 15.81C). Sheldon & Walker (1993a) examined the value of shell morphology for separating Australian species of *Notopala*. Smith (1992) recognised the above three genera, *Centrapala*, *Larina* and *Notopala*, and listed six endemic species: *Centrapala lirata*, *Larina strangei*, *Notopala essingtonensis*, *N. hanleyi*, *N. sublineata* and *N. waterhousii*.

Comprehensive anatomical studies of Australian species are lacking. Stoddart (1982) stated that the anatomy of the widespread *Notopala essingtonensis* and the northern Australian *N. waterhousii* is essentially the same as recorded by Vail (1977) for bellamyinine genera, but provided no details. The mantle cavity has a monopectinate ctenidium and an osphradium. The radula is small with a squarish multicuspidate central tooth and serrate, lateral and marginal teeth (Fig. 15.81D; Benthem Jutting 1956, 1963).

Sexes are separate. The male has a modified right tentacle which acts as a copulatory organ. Females are ovoviviparous and embryos develop in a uterine brood pouch. Stoddart (1982) reports quite distinct reproductive strategies for *Notopala essingtonensis* and *N. waterhousii*. The former species lives in permanently wet situations and produces batches of young continuously, whereas *N. waterhousii* lives in habitats that experience seasonal drying and produces batches of young sporadically in response to favourable conditions.

Viviparids are found in mud bottoms in lowland rivers and lakes (Cotton 1935a, 1935b). They are typically widespread, but two species, *N. hanleyi* and *N. sublineata*, which were once widespread in the Murray-Darling river system, are now severely restricted due to river control (Sheldon & Walker 1993a, 1993b); *Notopala hanleyi* persists in irrigation pipelines in South Australia and *N. sublineata* still lives in the Lake Eyre Basin. No

information is available on food of Australian viviparids and life histories have yet to be studied. In South-East Asia, viviparids act as intermediate hosts for echinostomous trematodes (Malek & Cheng 1974). However, no such association has yet been recorded in Australian species.

Species of *Notopala* are widespread in the north of the continent, but extend south in the eastern states; the genus *Centrapala* is only found in the Lake Eyre Basin; and *Larina* occurs in eastern Queensland. McMichael (1967) postulated that the Australian species originated in the Indo-Malayan area, a view supported by Stoddart (1982) who based his conclusions on the similarities in shell and anatomy of these two groups. *Larina strangei* from eastern Australia is probably a local derivative of more generalised *Notopala*-like ancestors.

A single fossil species, *Notopala wanjakalda*, has been recorded (Cotton 1935a) from Pleistocene sediments near Murray Bridge, South Australia. In North America, viviparids have been recorded from Upper Cretaceous sediments (Wenz 1938–1944).

Order SORBEOCONCHA

This group includes all caenogastropods with the exception of the Architaenioglossa. It is characterised by a primarily inhalant flow into the pallial cavity (hence the name) which is often associated with an inhalant siphon or notch, an epiathroid nervous system, a large osphradium with Si cells and lateral ciliated ridges and a secondary larval shell (protoconch II) associated with planktotrophic feeding. It includes many of Thiele's (1929–1935) Mesogastropoda and Stenoglossa (= Neogastropoda).

Superfamily CERITHIOIDEA

The Cerithioidea is one of the largest and most diverse superfamilies of the Caenogastropoda and one which has, since Cretaceous times, radiated extensively in marine, brackish-water and freshwater habitats. The group is particularly well represented in the tropics and subtropics, where species from widespread families such as the Cerithiidae ('sand creepers') and Potamididae ('mud whelks') may form the dominant molluscan component of shallow-water and intertidal ecosystems. Houbriek (1988), has estimated that there may be as many as 25 families with 200 genera. Typically, the shells are elongate, turreted and highly sculptured, and usually have an anterior siphonal notch or canal. Shell length ranges from small (3–10 mm) in the Litiopidae, Dialidae and Scaliolidae, to large (up to 100 mm or more) in some of the Potamididae, Cerithiidae, Siliquariidae and Turritellidae. In some taxa, the shells may be stocky and low-spined (littoriniform – Planaxidae; trochiform – Modulidae), or show reduced sculpture (Dialidae, Litiopidae), weak or no siphonal notch (Turritellidae, many Thiariidae, Dialidae, Litiopidae) or varying degrees of uncoiling (Siliquariidae and some Turritellidae). Most cerithioideans are microalgal grazers or detritus feeders, and have a taenioglossate radula, a pair of chitinous jaws, style sac and gastric shield, epiathroid nervous system, monotocardian heart, monopectinate ctenidium and corneous operculum (multi- or paucispinal). The gonad overlies the digestive gland in the visceral coil. Two families, the Turritellidae and Siliquariidae, are largely or exclusively filter-feeding.

Cerithioideans can be distinguished from other neotaenioglossans (and all other caenogastropods) by the following suite of anatomical characters: (1) open pallial gonoducts (sometimes partially closed in females; totally closed in the freshwater family Thiariidae); (2) aphaallic males (penis rarely present); (3) production of spermatophores (Fig. 15.82A); and (4) presence of uniflagellate euspermatozoa (Fig. 15.82B) with four straight mitochondria (each with parallel cristal plates; Fig. 15.82D–F) and posteriorly multiflagellate paraspermatozoa (Fig. 15.82C).

Much of the taxonomy of the superfamily has in the past been based on shell characters, but due largely to the work of Houbriek (see references herein 1971–1993), detailed anatomical studies

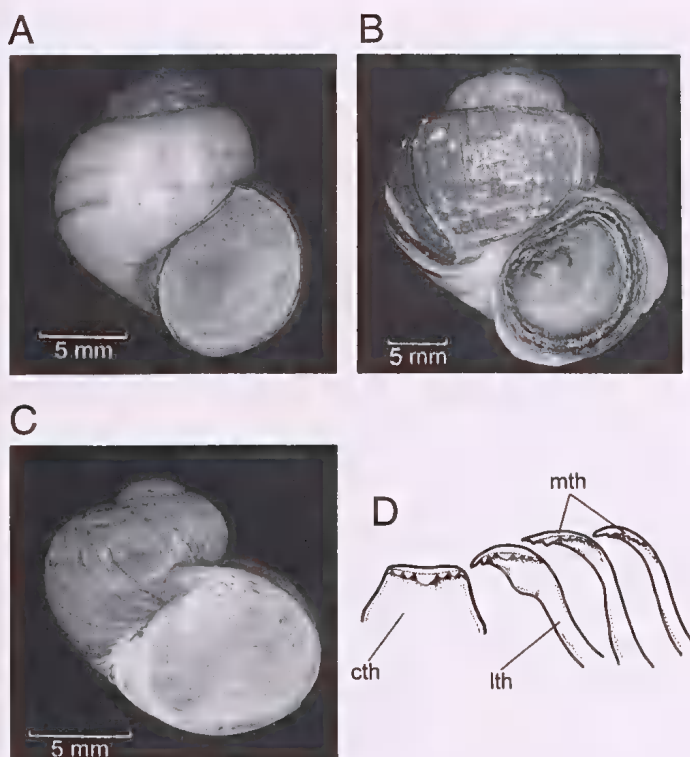


Figure 15.81 Family Viviparidae. A–C, shells, apertural view: A, *Notopala essingtonensis*, from northern Queensland; B, *Notopala waterhousii*, from the Northern Territory; C, *Larina strangei*, from south-eastern Queensland. D, *Bellamyja javanica* from Java, half a transverse row of the radula. cth, central tooth; lth, lateral tooth; mth, marginal teeth. (D, after Benthem Jutting 1956) [A–C, Queensland Museum; D, B. Scott]

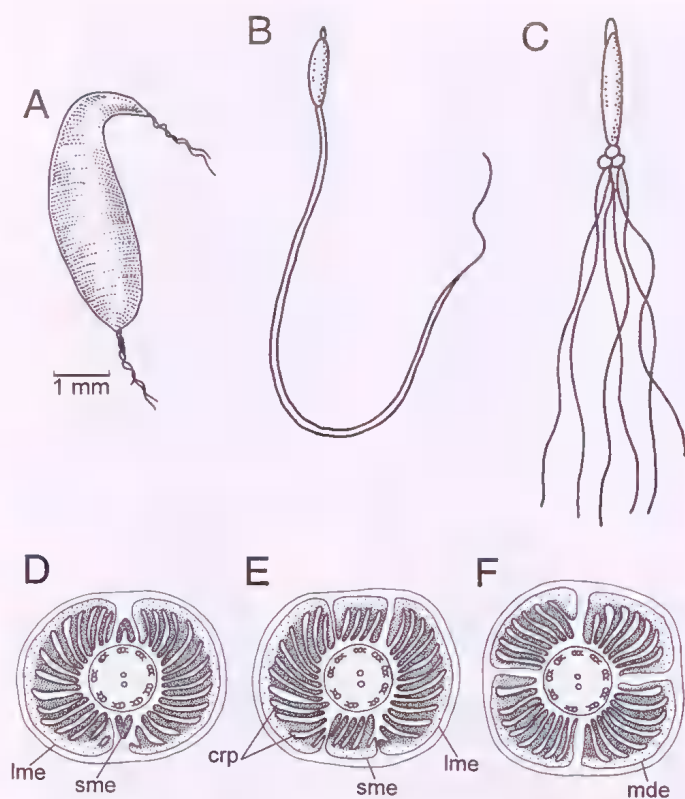


Figure 15.82 Superfamily Cerithioidea. A, *Cerithium eburneum* (Cerithiidae), spermatophore. B, C, dimorphic spermatozoa: B, uniflagellate euspermatozoon; C, multiflagellate paraspermatozoon. D-F, cross-sections of euspermatozoa at the midpiece region showing the arrangement of the mitochondrial elements and cristall plates; these show the features of the three groupings within Cerithioidea: D, Group 1(subgroup i), includes Cerithiidae, Turritellidae, Siliquariidae, Dialidae and Litiopidae; E, Group 1(subgroup ii), includes Batillariidae and Planaxidae; F, Group 2, includes Potamididae, Modulidae, Scaliolidae, Thiaridae and Pachychilidae. crp, cristall plates; lme, large mitochondrial element; mde, mitochondrial elements of equal size; sme, small mitochondrial element. (A-C, after Houbrick 1973; D-F, after Healy 1983) [A.J. Hill]

and systematic reviews now exist for many of the major families and genera. Other notable contributions to the study of cerithioidean anatomy include those by Thiele (1929–1935), J.E. Morton (1951c, 1951d, 1953), J.E. Morton & Keen (1960), Ev. Marcus & Er. Marcus (1964a), Dazo (1965), Davis (1969, 1971, 1972), Starmühlner (1969, 1970, 1976, 1992, 1993), Driscoll (1972), Luque, Templado & Burnay (1988) and Ponder (1991b, 1994a). In a number of studies, ultrastructural aspects of the anatomy of cerithioideans, including the osphradium (Haszprunar 1985a, 1988a; see also Maeda 1986 for light microscopy of osphradium), spermatozoa and spermatogenesis have been examined (Giusti 1971; Healy & Jamieson 1981; Healy 1982b, 1982c, 1983, 1986a, 1986b, 1988a, 1988b, 1996; Kohnert & Storch 1984a, 1984b; Koike 1985; Hodgson & Heller 1990), and radulae (Houbrick several papers 1976–1993; Bandel 1984).

Several taxa have, in recent years, been removed from the Cerithioidea on the basis of anatomy and sperm ultrastructural evidence, thereby reversing a trend to use the superfamily as a convenient location for species, genera and families with cerithiiform shells, but unknown affinities. Those families removed include the following: Cerithiopsidae and Triphoridae (both now in Triphoroidea), Vermetidae (now in Vermetoidea), Campanilidae and Plesiotrochidae (both now in Campaniloidea), Abyssochrysidae (now in Loxonematoidea), Provannidae (now in either Loxonematoidea or Littorinoidea) (Fretter 1980; Healy 1988a, 1988b, 1990b, 1990d, 1993b; Ponder & Warén 1988; Houbrick 1989). The list of cerithioidean taxa given by Ponder & Warén (1988) includes 19 families with extant representatives and an additional seven families known only from the fossil record. Of the living families, the following are definitely known to occur in Australian waters: Diastomatidae, Scaliolidae (= 'Obortionidae' or 'Finellidae'), Dialidae, Litiopidae, Cerithiidae, Potamididae,

Batillariidae, Thiaridae, Planaxidae, Modulidae, Turritellidae and Siliquariidae. To this list may possibly be added the Melanopsidae, if Brandt's (1974) report of the genus *Faunus* from northern Australia can be confirmed; this genus occurs in South-East Asia and New Guinea, and conceivably in northern Australia (see Houbrick 1991 for discussion). Two families recognised by Ponder & Warén (1988) have never been recorded from Australia: Pachychilidae (formerly the Pleuroceridae) and Symolopsidae (cerithioidean status uncertain).

In spite of much recent progress in the study of small-sized cerithioideans (Litiopidae, Bittiinae, Dialidae, Scaliolidae – Houbrick 1987b, 1993a; Luque *et al.* 1988; Ponder 1991b, 1994a; Ponder & de Keyser 1992) the taxonomic position and anatomy of several genera remain poorly known. The need for such work is especially important as there has been over-reliance on sometimes highly convergent shell characters for defining groups, resulting in either weakly defined or completely spurious higher taxa. It should, for this reason, be emphasised that cerithioidean families are usually diagnosed on the basis of an entire suite of characters, and that when trying to place species or genera within families it is necessary to consider all features (shell, operculum, radula, anatomy, fine structure, *etc.*). Nevertheless, we have in this account indicated obvious external differences between families and between major genera (operculum and shell shape and sculpture and head-foot features) in order to facilitate ready identification.

Healy (1983) recognised two broad assemblages within the Cerithioidea based on euspermatozoan ultrastructural features. Group 1, with two small mitochondrial elements, consists of: Subgroup i (Fig. 15.82D) – the Turritellidae, Cerithiidae, *Australaba* (= *Alaba*, family Litiopidae – see Houbrick 1987b), Dialidae, Siliquariidae; Subgroup ii (Fig. 15.82E) Planaxidae and Batillariinae (Batillariidae). Group 2 (Fig. 15.82F) – is characterised by four equal-sized mitochondrial elements – Potamidinae (Potamididae), Modulidae and *Obortio* (now = *Finella*, family Scaliolidae; see Ponder 1994a). Relevant eusperm groupings are cited with each description of family characteristics in this text.

Cerithioideans are most common in tropical areas and individual species may be abundant. Most are marine, living in the shallow sublittoral or the intertidal zones and on a variety of substrata including sand, mud and sometimes rock or coral rubble. Some families, such as the Pachychilidae, Thiaridae and Melanopsidae, live in freshwater and several species of the marine families Cerithiidae and Turritellidae live in the deep water of the continental shelf and slope. A few families have adapted to specialised habitats, the Potamididae, for example, being largely confined to mangroves. In general, cerithioideans are herbivores or detritivores; only turritellids and siliquariids are known to be filter feeders (Houbrick 1988), but even among turritellids there are reports of herbivory and detritus-feeding (Allmon 1988). The sexes are usually separate, but protandric hermaphroditism and parthenogenesis occur within some families (protandry in some Turritellidae, possibly all Vermiculariinae, and possibly all Siliquariidae; parthenogenesis in most Thiaridae) (Jacob 1957; Starmühlner 1969; Berry & Kadri 1974; Carrick 1980a, 1980b; Bieler & Hadfield 1990). Males are generally aphallic (penis in some Pachychilidae and Siliquariidae – Boss 1982; Hughes, R.N. 1985a), produce dimorphic spermatozoa, packaged in spermatophores (Houbrick 1988; Kennedy 1995). Egg capsules are usually laid in gelatinous strings (folded and sometimes coiled in various configurations and often combined with sand or mud particles) from which young emerge as free-swimming veligers (planktotrophic or lecithotrophic) or as crawling juveniles (that is, direct developers). Some families, such as the Turritellidae, Planaxidae and Thiaridae, are ovoviviparous or viviparous, utilising cephalic or pallial brood pouches.

The Cerithioidea is an ancient group, almost certainly arising sometime in the Palaeozoic (Cox, L. 1960a). The exact period of origin is still uncertain, but most extant families were established by the late Cretaceous or early Tertiary (Houbrick 1981a, 1988).

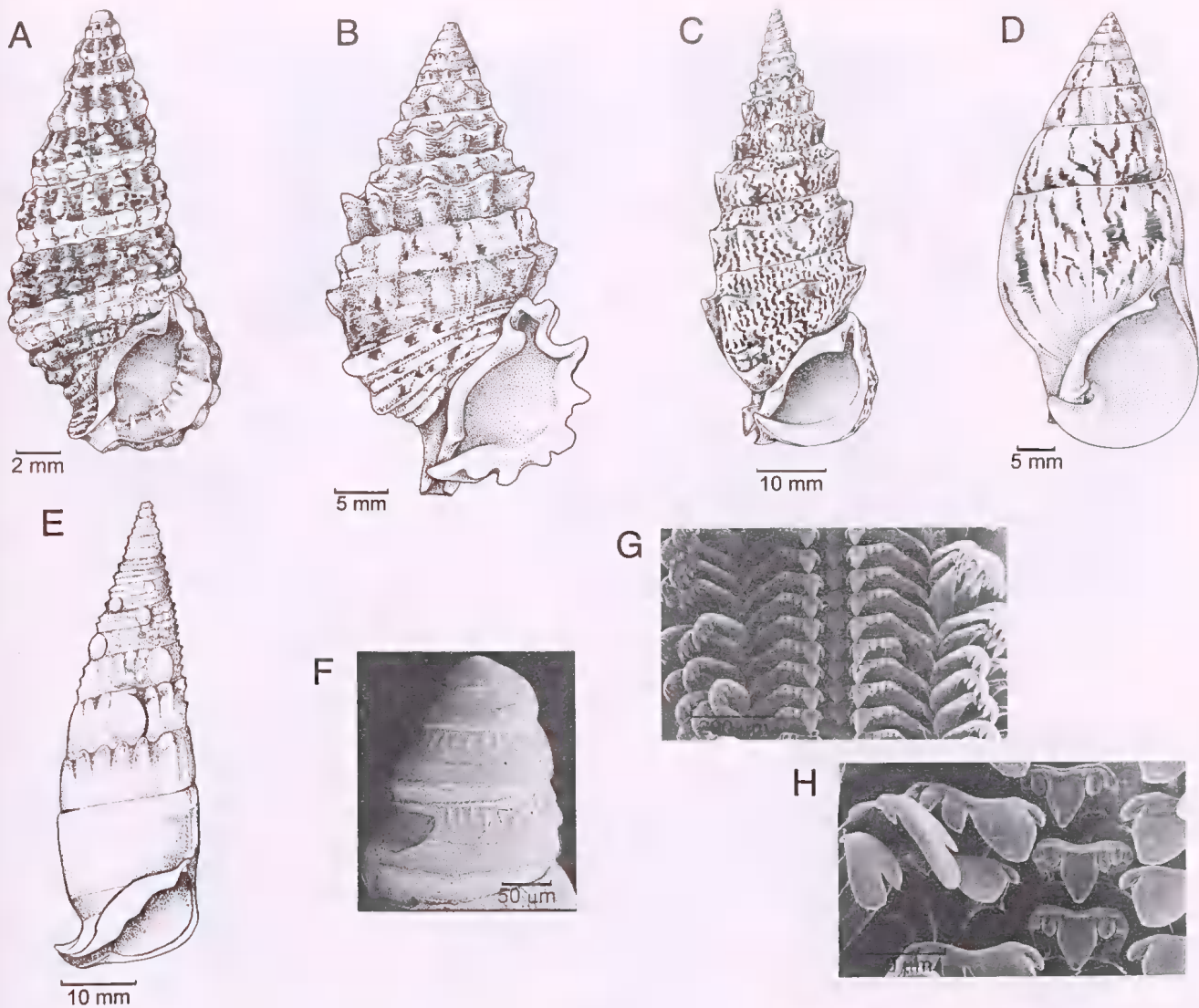


Figure 15.83 Family Cerithiidae, subfamily Cerithiinae. A–E, shells, apertural view: A, *Clypeomorus bifasciata*; B, *Cerithium echinatum*; C, *Pseudovertagus aluco*; D, *Gourmya gourmyi*; E, *Rhinoclavis vertagus*. F, *Cerithium* sp., protoconch showing the sinusigeral notch. G, H, portions of radula of *Cerithium citrinum*: G, a number of transverse rows of radular teeth with the marginal teeth folded back; H, details of the central and lateral teeth. (F–H, from Houbrick 1992a)

[A–D, R. Plant; E, G. Parker]

By then cerithioideans had radiated extensively into several habitats – marine, estuarine and brackish-water lagoons; freshwater lakes and streams; marine intertidal and rocky shore; coral reefs and associated sand patches and rubble; deep-sea muddy habitats (Houbrick 1980d, 1988). Most families have remained diverse to the present day, but a few, such as the once speciose Diastomatidae – now represented by a single living species (Houbrick 1981c), have declined dramatically.

Attempts to evaluate relationships between families within the Cerithioidea, and between the Cerithioidea and other caenogastropods, have only proved useful after the elimination of families erroneously assigned to the superfamily (among them the Triphoridae, Cerithiopsidae, Vermetidae, Campanilidae and Plesiotrochidae). Healy (1983) found that euspermatozoan ultrastructure, especially the structure of the midpiece region, was valuable not only for associating groups of cerithioidean families (see above for listing) but also for helping to define the Cerithioidea. Houbrick (1988) and Ponder (1991b) have presented cladistic analyses of the Cerithioidea based on shell and anatomical characters. Although points of similarity between the two cladograms are emerging from these studies (Planaxidae + Thiariidae + Diastomatidae assemblage and Pachychiliidae + Melanopsidae assemblage), there are also many differences (Ponder's analysis essentially reverses Houbrick's tree). Such differences probably derive from the characters used for analysis (although Ponder did use many of Houbrick's characters), the selection of an outgroup (Rissooidea or Stromboidea by Houbrick; Rissooidea or Campaniloidea by Ponder) and differing perceptions of the scope of the Cerithioidea (Campanilidae and

Vermetidae included by Houbrick; Ponder excluding these families and adding Dialidae to the analysis). Almost certainly the use of additional taxa (for example, Scaliolidae) and characters (sperm and other ultrastructural features), in combination with DNA/RNA analysis will help greatly in achieving a better understanding of relationships within this large superfamily.

Family Cerithiidae

The Cerithiidae, by far the largest family within the Cerithioidea, comprise two subfamilies (Cerithiinae, Figs 15.83, 15.84, and Bittiinae, Fig. 15.85), several genera (25 or more) and, according to Houbrick (1988), many hundreds of species. Cerithiidae are marine and occur worldwide, generally in shallow water in subtropical and tropical regions. Some genera, however, occur only in moderate to great depths (for example, *Varicopeza*, *Argyropeza* – Houbrick 1980b, 1980c), but such taxa never contain more than a few species. Cerithiids inhabit a variety of substrata including sandy and/or coral rubble areas among coral reefs, sand flats, or more rarely the seaward side of mangroves in sheltered bays. Species of the Indo-Pacific genus *Clypeomorus* live almost exclusively on hard substrata such as rock or rubble intertidally (Houbrick 1985). In some localities, particularly in the tropics, cerithiids may be the most abundant of the larger-sized molluscs. Most species appear to be microalgal-detritus feeders; the small differences in radular shape and cusping reflect the physical nature of the substratum being worked. Whereas shells of the subfamily Cerithiinae range in size from 10–114 mm (sometimes larger) with spiral, often nodulose sculpture and a well-defined anterior canal (Fig. 15.83A–E), those of

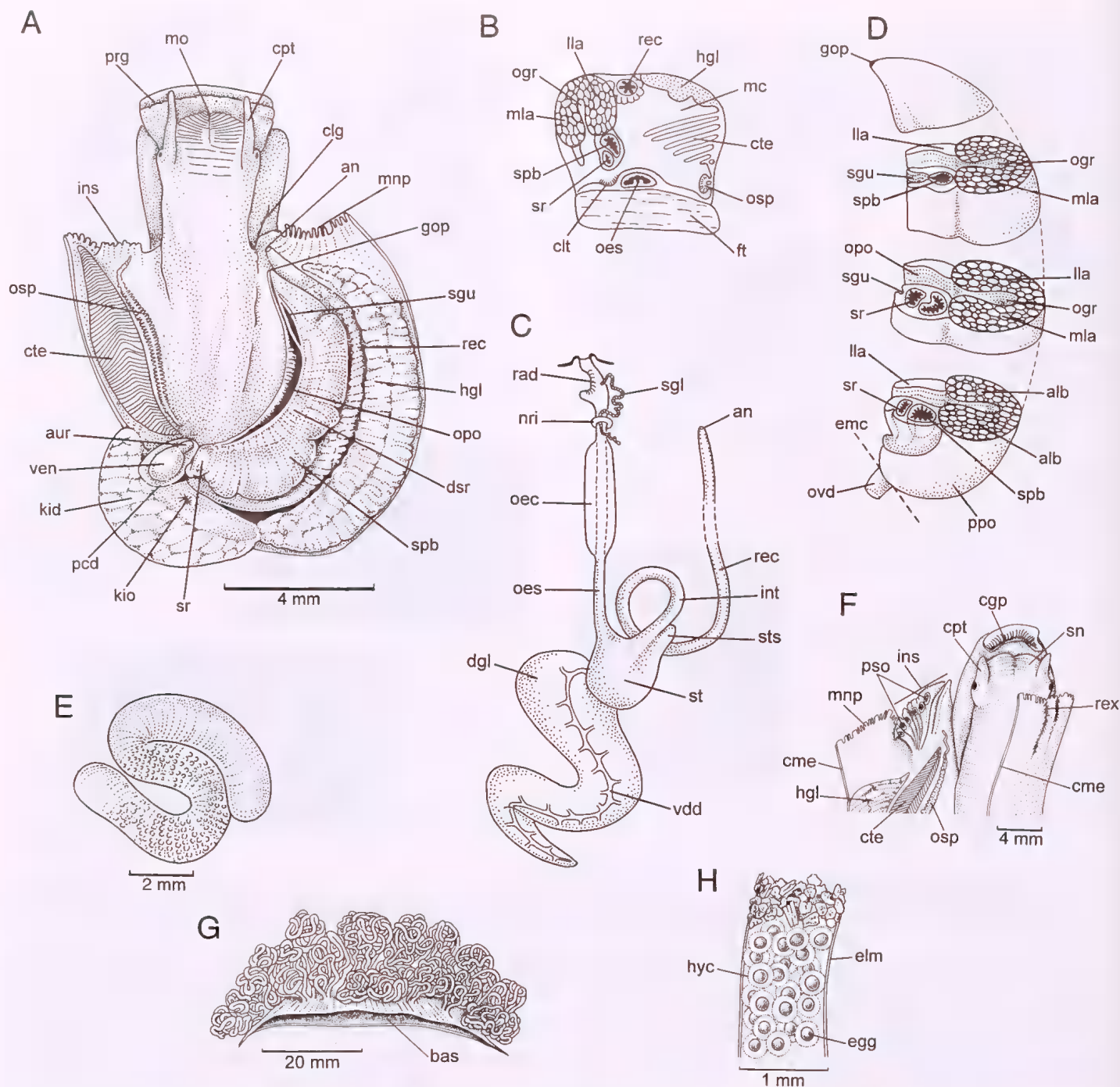


Figure 15.84 Family Cerithiidae, subfamily Cerithiinae. A–E, *Clypeomorus bifasciata*: A, female with mantle organs exposed by a dorsal longitudinal cut in the mantle – the visceral whorls have been removed and the kidney has been pulled back exposing the pericardium and proximal pallial oviduct; B, section through mantle cavity showing spatial relationship of the pallial oviducts to the other mantle organs; C, generalised alimentary tract; D, pallial oviduct of female, sectioned to show internal arrangement of ducts; E, egg mass, from Guam. F, *Gourmya gourmyi*, head and anterior part of mantle cavity exposed by dorsal longitudinal cut in mantle; note presence of pallial siphonal ocelli on the inhalant siphon. G, H, *Cerithium nodulosum*: G, egg mass detached from rocky substratum – the egg mass consists of a base to which clusters of many coiled filaments are attached; H, portion of filament with sand grains removed to show eggs. **alb**, albumen gland; **an**, anus; **aur**, auricle; **bas**, base of egg mass; **egp**, ciliated groove of propodium; **clg**, ciliated groove; **clt**, ciliated tract; **cme**, cut mantle edge; **cpt**, cephalic tentacle; **cte**, ctenidium; **dgl**, digestive gland; **dsr**, distal seminal receptacle; **egg**, egg; **elm**, external limiting of membrane; **emc**, end of mantle cavity; **ft**, foot; **gop**, gonopore; **hgl**, hypobranchial gland; **hyc**, hyaline capsule; **ins**, inhalant siphon; **int**, intestine; **kid**, kidney; **kio**, kidney opening; **lla**, lateral lamina; **mc**, mantle cavity; **mla**, medial lamina; **mnp**, mantle papillae; **mo**, mouth; **nri**, nerve ring; **oec**, midoesophageal crop; **oes**, oesophagus; **ogr**, oviducal groove; **opo**, opening to pallial oviduct; **osp**, osphradium; **ovd**, oviduct; **pcd**, pericardium; **ppo**, proximal pallial oviduct; **prg**, propodium groove; **psd**, pallial siphonal ocelli; **rad**, radula; **rec**, rectum; **rex**, ridge forming exhalant siphon; **sgl**, salivary gland; **sgu**, sperm gutter; **sn**, snout; **spb**, spermatophore bursa; **sr**, seminal receptacle; **st**, stomach; **sts**, style sac; **vdd**, ventral duct of digestive gland; **ven**, ventricle. (A–E, after Houbbrick 1985; F, after Houbbrick 1981b; G, H, after Houbbrick 1971) [R. Plant]

the subfamily Bittiinae only occasionally exceed 10 mm and are usually narrow with cancellate sculpture and a shallow or sometimes obsolete anterior canal (Fig. 15.85A, D). A few bittiine species, however, approach 20 mm in shell length, including the Australian *Cacozeliana granaria*, the largest living member of the subfamily (Fig. 15.85A; Houbbrick 1993a). Aside from shell differences, Houbbrick (1993a) noted that in the Bittiinae, unlike the Cerithiinae, some species have a well-developed epipodial skirt (Fig. 15.85E, H, I) and/or long epipodial tentacles, and, uniquely among cerithioideans, have three sites for sperm storage in the female (two seminal receptacles and one spermatophoral bursa).

Cerithiid shells have a turreted, multi-whorled teleoconch typically sculptured with spiral rows of nodules (strength variable depending on taxon) and/or axial ridges. An anterior siphonal canal is present and often well developed. The aperture is oval in shape and commonly with a thickened, flared outer lip (flaring moderate in most, but sometimes is very strong or very slight). The protoconch (Figs 15.83F, 15.85B) may have small or large whorls – the latter type indicative of direct development. Protoconch I consists of one to one and a half whorls and is usually smooth. Protoconch II consists of two or two and a half whorls, has a prominent sinusigeral notch, and is sculptured with a

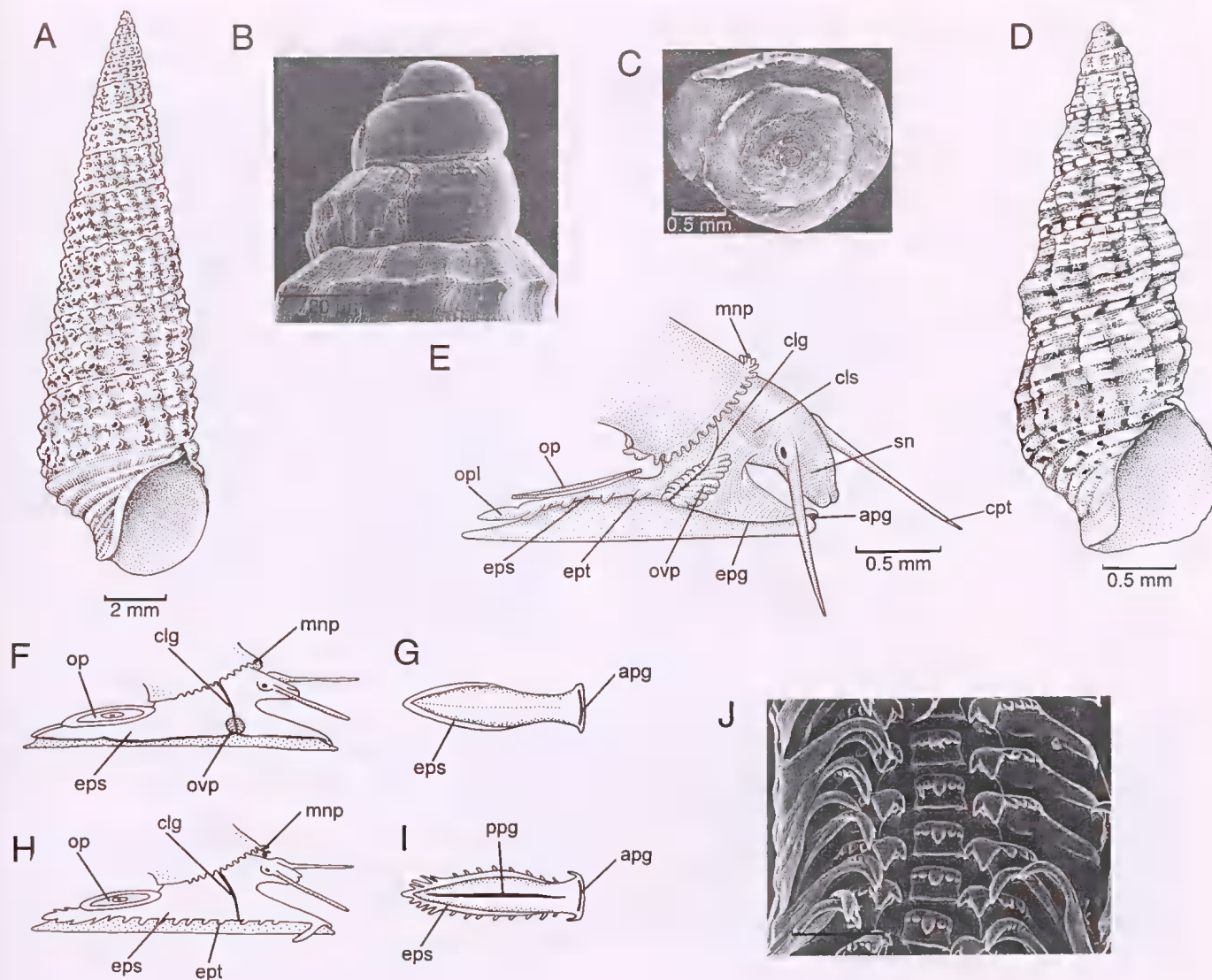


Figure 15.85 Family Cerithiidae, subfamily Bittiinae. A–C, *Cacozeliana granaria*: A, shell, apertural view; B, protoconch and apical whorls of teleoconch; C, operculum. D, *Ittibittium houbrieki*, shell, apertural view. E, *Bittium reticulatum*, external features of head-foot, right lateral view. F–I, external anatomical features of two genera, *Cacozeliana* (F, G) and *Ittibittium* (H, I): F, H, head-foot, right lateral view; G, I, soles of feet and epipodial skirt configurations. J, *Cacozeliana granaria*, mid-section of radula showing several transverse rows. apg, anterior pedal gland; clg, ciliated groove; cls, ciliated strip; cpt, cephalic tentacle; epg, epipodial groove; eps, epipodial skirt; ept, epipodial tentacle; mnp, mantle papillae; op, operculum; opl, opercular lobe; ovp, ovipositor; ppg, posterior pedal gland; sn, snout. [A, D, R. Plant; E–I, A.J. Hill]

variable number of spiral cords and often minute pustules and/or axial plaits (Fig 15.83F). The operculum is oval and corneous, with an eccentric nucleus (Fig. 15.85C).

The following summary of cerithiid anatomy is based principally on the work of Houbrick (1971, 1974, 1976b, 1977, 1980b, 1980c, 1981b, 1984b, 1985, 1988, 1992a, 1993a, 1993b) and diagnosis provided by Boss (1982). The head-foot (Figs 15.84A, 15.85E, F, H) features a short, broad snout, moderately long cephalic tentacles with an eye associated with the base of each tentacle, and has a short, broad to narrow foot which either lacks epipodial tentacles (Cerithiinae) or frequently has them (some Bittiinae; Fig. 15.85E). The shape of the jaws ranges from semicircular to ovate. Details of the radulae are illustrated in Figures 15.83G, H (Cerithiinae) and 15.85J (Bittiinae). Each tooth row of the radula has a central tooth with a prominent central cusp with two smaller cusps on each side. The shape of the central tooth is variable, but it is usually quadrate, and the basal plate sometimes has a basal protrusion, or, as in Bittiinae, has concave sides. The lateral teeth have one large cusp flanked by one small inner cusp and a variable number of small, outer cusps. The marginal teeth are curved to scythe-like with few to many small cusps. The mantle cavity (Fig. 15.84A, B) contains a long ctenidium, a long, weakly to strongly bipectinate osphradium, a hypobranchial gland and a renal organ as well as the rectum and the gonoduct. An oesophageal gland is present and the salivary glands pass through the nerve ring (Fig. 15.84C). The stomach has a style sac (Fig. 15.84C), crystalline style and gastric shield. The nervous system features short

connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion and long cerebropedal connectives. Zygoneury is usually absent. Pallial siphonal ocelli may sometimes be present (Fig. 15.84F). Cerithiids are dioecious. In females the gonoduct is glandular (with a capsule gland and an albumen gland) with one or two seminal receptacles and a spermatophoral bursa (Fig. 15.84B, D). An ovipositor may be present (Fig. 15.85E, F) or absent. Males have euspermatozoa typed as Group 1(i) of Healy (1983); and paraspermatozoa of basic cerithioidean type with an acrosome-like structure, condensed nuclear core surrounded by dense vesicles, midpiece and multiple (5–8) flagella – Healy (1986a). Eggs are laid in gelatinous, often winding strings (Fig. 15.84E, G, H). Development may be indirect or direct.

The shells of many cerithiids are variable in shape, sculpture and often colour, a fact that has led to taxonomic confusion and some corresponding devaluation of the significance of certain ecological studies. There is also evidence to suggest that hybridisation may occur between species or genetically distinct populations (Houbrick 1985, 1992a). Although several cerithiids may resemble batillariids and potamidids in shell shape, the morphology of the operculum immediately separates these taxa (operculum oval and paucispiral in Cerithiidae; circular and multispiral in Batillariidae and Potamididae). In addition, most batillariids and potamidids are euryhaline, occurring in the estuaries and mangrove swamps where few cerithiids are found.

Until recently, generic relationships in the Cerithiidae were poorly known. According to Houbbrick (1976a) about 70 generic and subgeneric combinations have been used for '*Cerithium sensu lato*' and 14 generic and subgeneric assignments have been used for the widespread Indo-West Pacific species, *Rhinoclavis sinensis*. Houbbrick in 1976a recognised six genera in the subfamily Cerithiinae: *Clavocerithium*, *Pseudovertagus*, *Rhinoclavis*, *Clypeomorus*, *Cerithium*, and *Liocerithium*. He later added another five genera: *Gourmya*, *Colina*, *Royella*, *Cerithioclava* and *Fastigiella* (Houbbrick 1981b, 1984b, 1986a, 1986c, 1987c, 1990c). All of the larger genera have now been monographed (Houbbrick 1976b, 1985, 1992a). Houbbrick (1993a) has reviewed the Bittiinae and recognised nine genera within the subfamily: *Bittium sensu stricto*, *Bittiolium*, *Ittibittium*, *Stylidium*, *Lirobittium*, *Cacozeliana*, *Argyropeza*, *Varicopeza* and *Zebittium*. Of these, the latter three were only provisionally included in the Bittiinae by Houbbrick in the absence of anatomical data. Houbbrick's cladistic analysis showed that *Cacozeliana*, although clearly belonging to the Bittiinae, shows much stronger affinity to the Cerithiinae than any other genus in the group. The genus *Ittibittium* is notable for its apparently disjunct distribution (one species recorded from south-western Australia and one species from Hawaii – see Ponder 1991b; Houbbrick 1993a). The Indo-Pacific Bittiinae have yet to be reviewed at the species level.

Approximately 60 cerithiid species are known from Australia. Cotton's 1960 list of the species recorded from the continent is now well out of date and contains several species now assigned to other families or superfamilies. Similarly, lists of species for individual States (New South Wales – Iredale & McMichael 1962; Tasmania – May 1923), although useful, are far from complete. Wilson (1993) listed, described, and in many cases, figured, most of the known, valid species from the Australian region based on recent literature (especially the monographs of Houbbrick). The major tropical shallow-water genera of the subfamily Cerithiinae represented in the Australian fauna are: *Cerithium* (about 23 species), *Rhinoclavis* (nine species), *Clypeomorus* (eight species), and *Pseudovertagus* (four or five species) (for monographic treatments of these genera see Houbbrick 1976b, 1985, 1992a). Most of these genera have members that are medium to large-sized and are now taxonomically, though not ecologically, well known. In contrast, the southern Australian cerithiids are small and with a few exceptions (see Ponder 1991b; Houbbrick 1993a) relatively poorly known taxonomically (all belong to the subfamily Bittiinae in various genera including *Cacozeliana*, *Ittibittium*, *Bittium sensu stricto* – see Houbbrick 1993a for further detail).

Although cerithiids mainly inhabit shallow water and many are large, well known species, there are also a number of deep-sea genera containing a few small-sized species that are poorly known anatomically. Houbbrick (1980c) reviewed the deep-water genus *Varicopeza*, which has a single species, *V. pauxilla*, living in Australian waters. A second deep-water genus *Argyropeza* contains five species, three of which occur off the Australian coast in depths to 914 m (Houbbrick 1980b). The genus *Glyptozaria*, previously placed, albeit with uncertainty (see Garrard 1972), in the Turritellidae, was shown by Houbbrick (1981d) to belong to the Cerithiidae; it contains two living species in Australian waters and one fossil species (*G. transenna*) from Victorian Middle Miocene. Even some shallow-water cerithiids are poorly known, as shown by the widespread distribution of *Royella sinon* from the Seychelles and Mauritius in the Indian Ocean to Pitcairn Island in the Pacific. Despite its wide range, records of this species from the Australian region are limited in museum collections to only six lots from Western Australia and Queensland (Houbbrick 1986a). *Gourmya gourmyi* is a large and distinctive cerithiid that inhabits shallow subtidal reef platforms including those of the Great Barrier Reef, but is still known from only a few localities (Houbbrick 1981b, 1984b).

Whereas several cerithioidean families are more or less tied to relatively narrow substratum preferences, the success of the Cerithiidae owes much to remarkable adaptive radiations within a variety of marine and estuarine habitats. The four most important were identified by Houbbrick (1980d) as: (1) subtidal sand lagoons;

(2) intertidal mud flats; (3) intertidal rubble flats; and (4) high intertidal shores. Despite their diversity, abundance and obvious ecological importance, little is known of the basic ecology of Australian cerithiids. The reproductive biology, seasonal clustering and trematode parasite stages of *Clypeomorus batillariaeformis* (as *Cerithium moniliferum*) were studied at Heron Island on the Great Barrier Reef by Moulton (1962), Cannon (1975, 1979) and Rohde (1981). In this species, ripe individuals occur throughout the year but are most numerous in spring, when eggs are deposited (a broad spawn ribbon containing 1500 to 2000 eggs). Much larger numbers of eggs (8800 to 85 000) occur in the egg masses of other *Clypeomorus* species and *Cerithium* species (see Houbbrick 1974; Rao & Ramasarma 1980). The young of *Clypeomorus batillariaeformis* grow rapidly, reaching 10 mm in the first year and migrating up the shore. A thickened outer lip is formed after one year and the animals spawn. Following spawning, growth and migration upshore are resumed. Murray (1969) described the spawn and early life history of *Cacozeliana granaria* (Bittiinae) which has planktotrophic veligers (see also Houbbrick 1993a). Yamaguchi (1977) examined growth and mortality rates of Guam populations of *Cerithium nodulosum*, a large-sized species common also in northern Australian reef waters. The animals reach their final adult size of 76 mm after about three years, but suffer moderate to heavy mortality in the juvenile stages. Houbbrick's (1974) observations on four *Cerithium* species from Florida indicate winter and spring spawning, with the young snails reaching maturity in about one year. Skilleter (1991, 1992) and Skilleter & Underwood (1993) have investigated larval recruitment in three species of *Rhinoclavis* and one species of *Cerithium* at One Tree Island. Their studies, which involved experimental manipulation of sediment particle size in the field, revealed that larval settlement was affected by the type of sediment present at any one site.

Cerithiidae extend back at least to the Upper Cretaceous (Houbbrick 1981a). All Australian fossils, however, are Tertiary in age or younger. Ludbrook (1971) recorded eleven species ranging from the Upper Eocene to the Pleistocene of southern Australia (Tasmania, Victoria, South Australia and Western Australia). These eleven species consist of nine assigned to *Theridium* (a subjective synonym of *Cerithium* – see Houbbrick 1992a) and two in the genus *Jetwoodsia*. *Semivertagus capillatus* and *Bittium (Semibittium) subgranarium*, both from the Australian Pliocene (see Ludbrook 1957) are probably also assignable to the Cerithiidae. Houbbrick (1976a, 1985, 1992a) recorded *Cerithium munitum*, *Cerithium punctatum* and *Clypeomorus bifasciata* from either the Holocene or Pleistocene of the west coast of Western Australia.

Family Dialidae

Until recently this family was poorly known both anatomically and taxonomically. The group consists of small cerithioideans of the genus *Diala*, species of which occur in marine and estuarine habitats in the Indo-West Pacific region. Dialids can be distinguished from other small-sized cerithioidean taxa (for example, Scaliolidae, Bittiinae, Litiopidae) by their often brightly spotted or flammulated shells that lack axial ribbing or an anterior siphonal notch. Members of perhaps the most closely related family, the Litiopidae, all have epipodial tentacles, whereas these are absent from all dialids.

Shells of *Diala* shells species are small, usually 5–7 mm or less in length, but measuring up to 14 mm in *D. suturalis* (Fig. 15.86A), with a high, conical spiral teleoconch consisting of several whorls (5.5 to 8). In addition, the shells are rather thick and opaque compared with those of many litiopids with which they may be confused. Sculpture is spiral only. The aperture is simple and lacks an anterior canal. The operculum is corneous and paucispiral with an eccentric nucleus (Fig. 15.86B). In most species, the protoconch is smooth initially (protoconch I) and with growth (protoconch II) develops a spiral ridge and is delineated from the teleoconch by a strong sinusigeral varix (Fig. 15.86D). *Diala megapicalis* has only an enlarged, smooth protoconch I (Fig. 15.86C), correlating with direct development of larvae within the egg mass (Ponder 1991b; Ponder & de Keyser 1992).

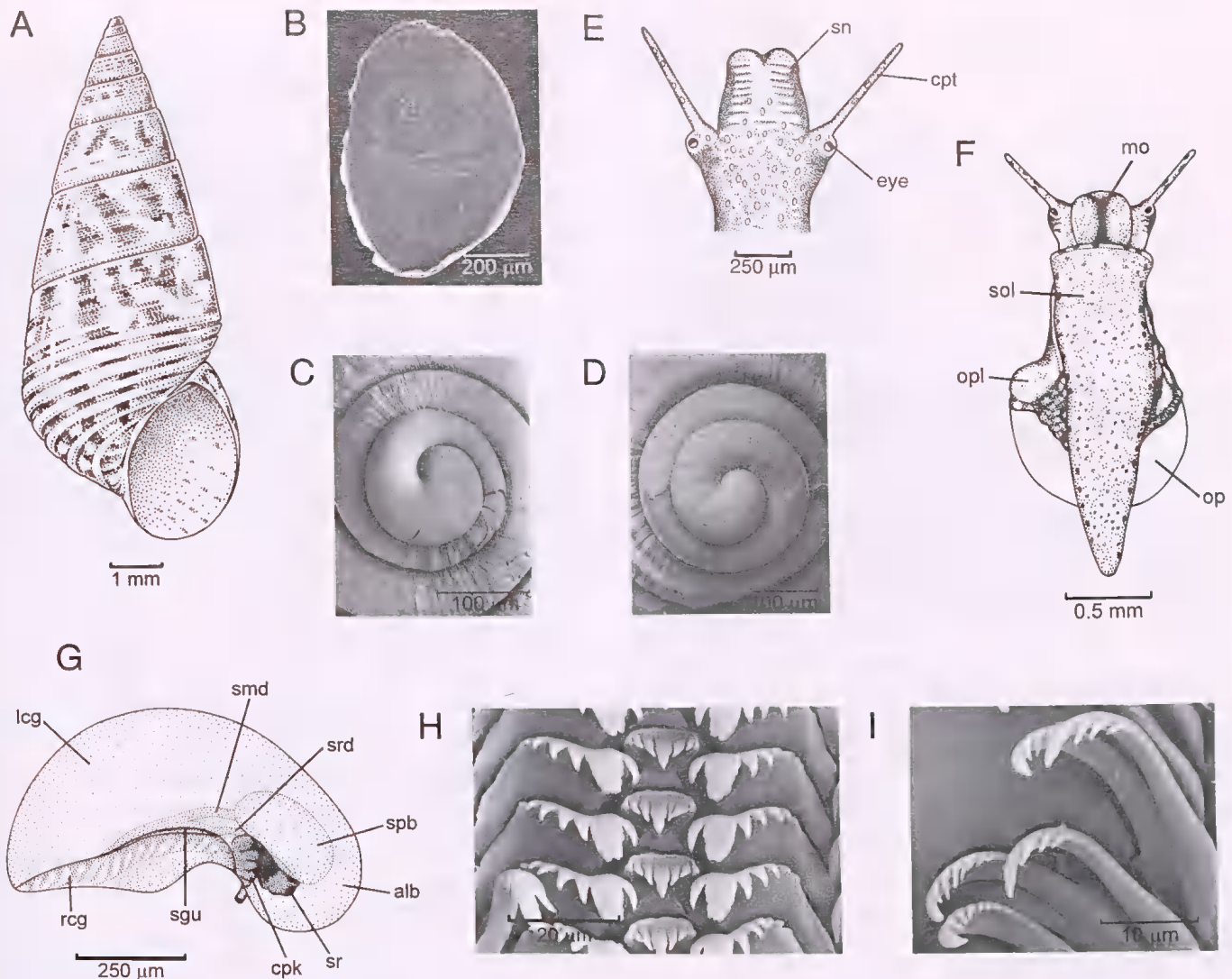


Figure 15.86 Family Dialidae. A, B, *Diallya suturalis*: A, shell, apertural view; B, operculum, inner surface. C, D, *Diallya megapicalis*; D, *Diallya albugo*. E, F, *Diallya sulcifera scobina*: E, head, dorsal view; F, animal, ventral view. G, *Diallya suturalis*, pallial glandular oviduct with associated organs and glands, left lateral view. H, I, *Diallya lirulata*, portions of radula: H, details of central and lateral teeth; I, details of marginal teeth. alb, albumen; cpk, ciliated pocket; cpt, cephalic tentacle; eye, eye; lcg, medial (left) lamella of capsule gland; mo, mouth; op, operculum; opl, opercular lobe; rcg, lateral (right) lamella of capsule gland; sgu, sperm gutter; smd, duct of spermatophore; sn, snout; sol, sole of foot; spb, spermatophore bursa; sr, seminal receptacle; srd, duct of seminal receptacle. (B, from Ponder 1991b; C, D, H, I, from Ponder & de Keyzer 1992; E, F, after Ponder & de Keyzer 1992; G, after Ponder 1991b)

[A, R. Plant; E–G, C. Eadie]

The following summary of dialid anatomy derives largely from the work of Ponder (1991b) for *Diallya suturalis* with additional details for other valid species provided by Ponder & de Keyzer (1992). The head features a short, broad and anteriorly bilobed snout, moderately long cephalic tentacles, with an eye positioned on a small bulge at the base of each tentacle (Fig. 15.86E). This region is variously pigmented depending on the species. The foot is long with a straight propodial edge and tapered posterior extremity (Fig. 15.86F), and has an anterior pedal gland, but no posterior pedal gland. Movement is achieved by ciliary gliding over the surface. The mantle cavity contains an elongate monopectinate osphradium, a ctenidium with distinct triangular filaments, and within the posterior region of the cavity, a renal organ, a well-developed hypobranchial gland, the rectum and gonoduct. A pair of jaws and the radular complex are contained within the buccal mass. Each tooth row of the radula (Fig. 15.86H, I) has a well-developed central tooth with a long, sometimes tricuspidate, central cusp, flanked on each side by three smaller cusps, and an hourglass-shaped basal plate with a simple basal edge without denticles. The strong lateral teeth have a long cusp flanked by one small cusp on the inner edge and four small cusps on the outer side. The curved marginal teeth have a long cusp on the outer edge with smaller cusps on the inner edge. The salivary glands are positioned on top of the nerve ring through which the anterior portion of the oesophagus passes. A large oesophageal gland is present. The

stomach is short and has a short style sac containing an ovoid crystalline style. Judging from the contents of the stomach of *Diallya suturalis*, dialids consume coralline algae, diatoms and probably general detritus. The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion, elongate extensions of the pedal ganglia and long cerebropedal connectives. It is uncertain whether a direct connection exists between the parietal and pleural ganglia (zygoneurous condition). Dialids are dioecious. The female gonoduct is glandular, closed proximally, with a sperm groove, seminal receptacle (associated with, but separated from, peculiar ciliated pockets) and spermatophore bursa (Fig. 15.86G). An ovipositor is absent. Euspermatozoa conform to Healy's (1983) Group 1(ii), and the paraspermatozoa are large and composed of a vermiform body filled with large dense vesicles and up to 90 axonemes, the axonemes emerging as flagella along the posterior third of the cell (see Fig. 1.17L; Tochimoto 1967; Healy 1986a). Ponder & de Keyzer (1992) described and illustrated the egg mass of *Diallya megapicalis*. This mass measures approximately 2 x 1.4 mm and contains between 30–45 eggs that take 14 days to hatch into crawling juveniles (Ponder & de Keyzer 1992). Protoconch morphology suggests that, with the exception of *D. megapicalis*, all other Australian species have planktotrophic larval development.

Diala species can be abundant in seagrass beds, on macroalgae or on coral rubble in the intertidal or shallow subtidal zones. Despite this abundance, no detailed studies of the ecology of dialids have yet been attempted.

Diala has in the past been placed by various authors in five different families of the Cerithioidea (the Litiopidae, Cerithiidae, Planaxidae, Diastomatidae, and Dialidae) and in the rissooidean family Rissoidae (for discussion see Ponder 1991b). Ludbrook (1941) first applied the name Dialidae, but unfortunately offered no diagnosis. Houbbrick (1981a, 1988) and Ponder & Warén (1988) listed the Dialidae as a separate family within the Cerithioidea, and subsequently, Ponder (1991b) and Ponder & de Keyzer (1992) provided a detailed diagnosis of the family and revised all nominal taxa. Four fossil genera linked by various authors with *Diala* have been dissociated and/or transferred elsewhere by Ponder & de Keyzer (*Dialopsis*, *Mereldia* – to Diastomatidae; *Paradiala* – possibly associated with Vanikoridae; *Melliwestea* – affinities undetermined).

Ponder (1991b) provided the first detailed anatomical study of what at the time was an unidentified species of *Diala* from Albany in south-western Australia; it is now known to be *D. suturalis* (Ponder & de Keyzer 1992). Two internal anatomical features of *Diala* set the genus apart from all other cerithioideans – firstly the distinctive paraspermatozoan morphology (see Fig. 1.17L; Tochimoto 1967; Healy 1986a) and secondly the presence of ciliated pockets associated with, but separate from, the seminal receptacle (Fig. 15.86G; Ponder 1991b). Healy (1986a) examined sperm ultrastructure and found that although the euspermatozoa of *Diala* are similar to those of the cerithioidean families Cerithiidae, Turritellidae, Litiopidae, and Siliquariidae, the paraspermatozoa are of a type unique within the Cerithioidea and contain up to 90 axonemes (see below and Healy 1986a). Other features, in combination, help to separate the Dialidae from other cerithioideans, including a small, tall-conspiral shell showing spiral sculpture only and an ovate aperture lacking an anterior canal; a smooth protoconch or one with a median spiral ridge; a paucispiral operculum with an eccentric nucleus; long cephalic tentacles; and the lack of an ovipositor and brood pouch (Ponder 1991b). Ponder (1991b) generated a cladogram of the Cerithioidea using the data provided by Houbbrick (1988) with modifications for the Dialidae. This showed the Dialidae to be most closely related to the Litiopidae – a conclusion at least consistent with euspermatozoan ultrastructure, despite the massive differences in paraspermatozoan morphology between dialids and litiopids (Healy 1983, 1986a).

Laseron (1956a) was the first author to attempt any overview of *Diala* from the Australian region, and included the genus within the Rissoidae – being apparently unaware of Thiele's (1929–1935) inclusion of *Diala* in the Cerithioidea. He described, from shells only, nine new species from northern Queensland. The taxonomy of *Diala* at the species level has been reviewed by Ponder & de Keyzer (1992) based on extensive museum holdings. Shells of each species of *Diala* are variable, and some of the recognised species have several synonyms, all of the species from Laseron's 1956a paper disappearing into synonymy. Of the 30 names that have been introduced, Ponder & de Keyzer (1992) recognised only six valid species (one with three geographically isolated subspecies) including a new species, *D. megapicalis*, from southern Australia. All six *Diala* species occur in Australian waters. Three are widespread (*D. semistriata*, *D. albugo*, *D. sulcifera*) in the Indo-West Pacific and three are endemic to Australia (*D. suturalis*, *D. megapicalis*, *D. lirulata*).

The genus *Diala* is known as a fossil from the early Miocene of the Eniwetok and Bikini Atolls (Ladd 1972). Extant species recorded as Pleistocene and/or Holocene fossils from Australia include: *Diala semistriata*, *D. suturalis*, *D. megapicalis*, *D. sulcifera scobina*, *D. lirulata* (Ponder & de Keyzer 1992; see also Ludbrook 1984). The fossil genus *Mereldia*, which was treated as a subgenus of *Diala* by Ludbrook (1957), is probably referable to the Diastomatidae (see Ponder & de Keyzer 1992).

Family Litiopidae

Litiopids constitute a distinctive family of small-sized cerithioideans (Houbbrick 1987b) that occur, often in large numbers, on algae and seagrasses in shallow, warm-temperate and tropical seas worldwide. The two recognised genera, *Alaba* and *Litiopa*, have on many occasions been placed in a variety of families (for example, Dialidae, Planaxidae, Cerithiopsidae), but most often are grouped as a subfamily of the Cerithiidae. Houbbrick (1987b) has studied in detail a species of each genus from Florida, thereby providing the first substantial account of litiopid anatomy and biology based on living and preserved animals. Supplementary data have also been published by Luque *et al.* (1988). Houbbrick (1987b) tentatively synonymised the following Australian genera under *Alaba*: *Diffalaba*, *Australaba* and *Dialessa*. The Australian litiopids are poorly known, but there are about ten named species and both *Alaba* and *Litiopa* are represented in the fauna. Litiopids are only likely to be confused with other small-sized cerithioideans living on algae or seagrass – namely members of the cerithiid subfamily Bittiinae and the Dialidae. Litiopids differ from both of these groups by having well-developed, sometimes very elongate, epipodial tentacles (tentacles weakly developed in Bittiinae, absent in Dialidae), and in having smooth or poorly sculptured shells (strong spiral and often axial ribs in Bittiinae) that show at best only slight traces of patterning (small subsutural spots or flammules, in contrast to the often strong patterning in Dialidae).

The litiopid teleoconch is typically thin (or transparent) and polished, turreted, multispiral and composed of 5 to 8 whorls (Fig. 15.87A, B). The aperture is ovate with a weakly developed anterior siphonal notch and a columella which is either smooth (*Alaba*) or has a small, low tooth (*Litiopa*). Sculpture is spiral and generally weak. The protoconch (Fig. 15.87C) is smooth initially (protoconch I) and with growth (protoconch II) becomes sculptured with axial plaits and one or more weak spiral cords. Protoconch II is delineated from the teleoconch by a strong sinusigeral notch (Robertson 1971b; Houbbrick 1987b; Luque *et al.* 1988). Periostracum is present on the teleoconch but is thin and transparent. The operculum is ovate, corneous, transparent to translucent and paucispiral with an eccentric nucleus (Fig. 15.87D).

The following summary of litiopid anatomy derives largely from the work of Houbbrick (1987b) and Luque *et al.* (1988) who have examined Atlantic species of *Alaba* and *Litiopa*. The head (Fig. 15.87E) features a relatively short, but extensible, conical and anteriorly bilobed snout, a pair of long cephalic tentacles (with red-brown stripes in *Alaba*) each with an eye at the base. The eyes of *Litiopa* are very small. The foot (Fig. 15.87E) is long with a convex propodial edge and tapered posterior (metapodial) extremity, and is equipped with both anterior and posterior pedal glands; the latter are capable of producing a strong mucous thread for emergency anchorage to algae or seagrass in case of dislodgment. Epipodial tentacles (sometimes very elongate) are associated with the propodium and the sides of the foot. The mantle edge is smooth. The mantle cavity contains an elongate, simple osphradium (running the length of the cavity), a large, ctenidium with long, triangular, heavily ciliated filaments, a narrow, thick hypobranchial gland, the rectum, a renal gland; and the gonoduct.

A pair of semicircular jaws and the radular complex are contained within the large buccal mass. Each tooth row of the radula (Fig. 15.87F, G) has a well-developed central tooth, strong lateral teeth and long, terminally scythe-shaped marginal teeth. The central tooth has a cutting edge with a long central cusp flanked on each side by two or three smaller cusps, and an hourglass-shaped basal plate. The lateral teeth have a long cusp flanked by two or three smaller cusps on the inner edge and four smaller cusps on the outer edge. The inner marginal teeth have a long cusp associated with the inner edge as well as two smaller cusps, and one small cusp on the outer edge. The outer marginal teeth have four to nine small cusps.

The paired, uncoiled salivary glands begin behind the nerve ring, but, anteriorly, pass through this ring. An oesophageal gland is present. The stomach features a large central ridge, gastric shield,

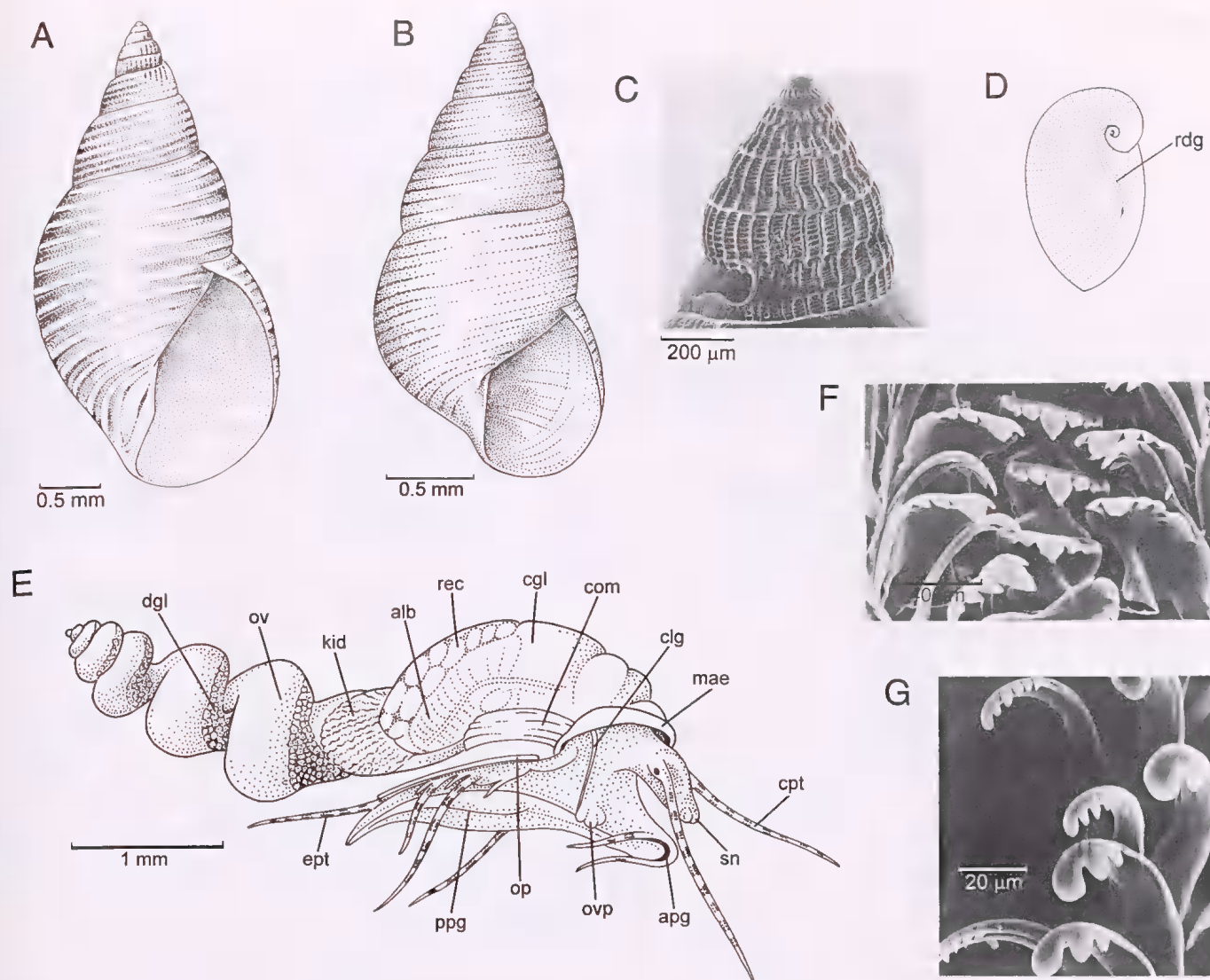


Figure 15.87 Family Litiopidae. A, B, shells, apertural view: A, *Litiopa* sp.; B, *Alaba opiniosa*. C, *Litiopa melanostoma*, protoconch showing cancellate sculpture and sinusigeral notch. D–G, *Alaba incerta*: D, operculum, outer surface showing sinuous attachment ridge by transparency; E, female viewed from the right side, showing the ovipositor, ciliated groove and long epipodial tentacles; F, details of central and lateral radular teeth; G, details of inner and outer marginal radular teeth. alb, albumen gland; apg, anterior pedal gland; cgl, capsule gland; clg, ciliated groove; com, columellar muscle; cpt, cephalic tentacle; dgl, digestive gland; ept, epipodial tentacles; kid, kidney; mae, mantle edge; op, operculum; ov, ovary; ovp, ovipositor; ppg, posterior pedal gland; rdg, attachment ridge; rec, rectum; sn, snout. (C, F, G, from Houbbrick 1987b; D, E, after Houbbrick 1987b)

style sac and probably a crystalline style. The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion and long cerebropedal connectives. Zygoneury is absent. Statocysts are associated with each pedal ganglion. Litiopids are dioecious. The female gonoduct is glandular, much wider than the male gonoduct and features a very well-developed albumen gland (proximally) and a capsule gland (distally). The free medial lamina of the female gonoduct has a sperm groove, the lateral lamina has a possible seminal receptacle. The presence or absence of spermatophores or spermatophoral receptacles has yet to be determined. Euspermatozoa conform to Healy's (1983) Group 1(ii), and the paraspermatozoa are essentially of the basic cerithioidean type but with a longer head region (length 30 µm) (Healy 1986a). Eggs are laid in a transparent, gelatinous ribbon shaped into a clockwise spiral egg mass of one to four turns (4.8–6 mm in diameter in *Alaba*, 2.5 mm in diameter in *Litiopa*). Eggs of *Alaba* are surrounded by a hyaline capsule (diameter 80 µm) and enclosed in a gelatinous chamber (diameter 130 µm). In *Alaba*, the egg mass is estimated to contain about 4800 eggs. Development is rapid, with the trochophore stage being reached in two days and the veliger in three. The egg masses degenerate at about six days, allowing the young to emerge as free-swimming veligers. The planktotrophic veliger is probably long lived as evident from the multiwhorled protoconch with a pronounced sinusigeral notch.

To date there have been no studies on the ecology of Australian litiopids even though several common species are present in the fauna. For example, species of *Alaba* are very common associates of algae and seagrasses around much of Australia. *Litiopa* is semipelagic, living in floating *Sargassum* and associated with algae attached to floating pumice. Specimens are often washed up on beaches in New South Wales and Queensland (W.F. Ponder personal communication). Scheltema, Williams & Tharpe (1989) plotted the abundance and distribution of pelagic larvae of *Alaba incerta* and *Litiopa melanostoma* in the Caribbean–Gulf of Mexico–northern South America area. Their study, based on collections gathered over a 12 year period, revealed that larval numbers reflect adult habitat – *Alaba* larvae being most common near the shore (adults live on seagrass), *Litiopa* being most common well offshore (adults live on floating *Sargassum* banks). It is not known if the larvae of Australian species of *Alaba* and *Litiopa* exhibit similar distribution patterns.

The family Litiopidae shows many similarities to the Dialiidae, and a recent cladistic analysis by Ponder (1991b) suggests that these families are closely related. As litiopid paraspermatozoa show none of the specialisations seen in dialid paraspermatozoa, and instead resemble more closely those of families such as the Cerithiidae, Batillariidae, Turritellidae and Planaxidae, it seems likely that the Litiopidae arose earlier than the Dialiidae. There are no published fossil records of litiopids from Australia.

Family Turritellidae

The Turritellidae are a large cosmopolitan family of cerithioideans, that live from the subtidal zone (rarely in upper littoral) to deep water (continental slope), generally on soft muddy-sandy bottoms, but also among gravel, shell grit or occasionally wedged among rocks. They may be the most abundant molluscan element in the benthos, with reports of depths to 200–10 000 m² for certain species (see Allmon 1988 for a comprehensive listing of sources). The shells (Fig. 15.88A, B) are small to very large (9–170 mm in length) with a narrow, turreted spire (numerous spirally sculptured whorls), often a broad, V-shaped sinus in the outer lip and a very weak or no anterior siphonal notch (for photographs of a range of Australian species see Garrard 1972 and Wilson 1993). Turritellids, like the closely related Siliquariidae, are all suspension-feeders but probably supplement food intake through deposit-feeding (Carrick 1980a; Allmon 1988). All are free-living, with the exception of species of *Vermicularia* which may, after a free-living juvenile stage, cement themselves to various hard substrata such as coral, or live within sponges (Morton, J.E. 1953b; Gould 1969; Bieler & Hadfield 1990). Aside from shell features, turritellids can be recognised by the following suite of characters: presence of mantle papillae (sometimes foliate) at the entrance to the mantle cavity (Fig. 15.88C, D); round, multispiral operculum (sometimes with peripheral bristles) (Fig. 15.88C); euspermatozoa of Group 1(i) that pair at the head region (Fig. 15.88H).

Turritellids have a long, multi-whorled, narrowly turreted shell that is usually sculptured with strong spiral cords (crossed in some species with weak axial ribs to give cancellate sculpture). The aperture profile is angled or rounded, shows a very weak or no anterior siphonal notch and has an outer lip often featuring a broad, backwardly directed sinus. Protoconch morphology is variable – typically those forms with pelagic larval stages have a small, multispiral protoconch I, whereas those with direct (or inferred direct) development have a large, paucispiral protoconch I. Allmon (1988) notes that during the transition from protoconch I to II there is no clear point of demarcation. In addition, turritellid protoconchs do not show a sinusigeral notch during the transition from protoconch II to the teleoconch (this contrasts with most other cerithioideans). The periostracum is usually thin and brown-tan in colour. The operculum is multispiral, and smooth or has peripheral bristles.

The following diagnosis of the Turritellidae has been compiled from several sources including Randles (1900), Graham (1938), Yonge (1946), J.E. Morton (1953b), Carrick (1980a, 1980b), Boss (1982), Allmon (1988), Houbriek (1988), Bieler & Hadfield (1990), Kennedy & Keegan (1992) and Kennedy (1995). The head-foot features a short, wide snout; a pair of long cephalic tentacles each with an eye situated near the tentacle base (Fig. 15.88D); a short foot with a ciliated groove on the right side. The entire mantle edge is ornamented with numerous papillae, that are often of disparate sizes (Fig. 15.88C, D). The mantle cavity (Fig. 15.88E) has an elongate, ridge-shaped, simple, osphradium; a long ctenidium with long filaments (a key structure in the suspension-feeding process); a series of pallial processes, arranged in rows and often foliate; a well-developed hypobranchial gland lacking distal leaflets; a renal organ; the rectum; and the gonoduct. A pair of thin weak jaws are present. Each tooth row of the radula has a quadrate, central tooth with a strong, serrated central cusp and a broad basal plate with a slightly convex basal edge. The lateral teeth have a large cusp flanked by many small outer cusps, and the marginal teeth are curved with numerous fine, small cusps. Some species have a modified taenioglossate radula with the number of marginal teeth varying from zero to three (3–0+1+1+0–3) (Boss 1982). A pair of uncoiled salivary glands are positioned above and anterior to the nerve ring. Oesophageal glands are present. The stomach features a short style sac, a crystalline style and a gastric shield. Turritellids are primarily ciliary-mucous suspension-feeders (Fig. 15.88F), their diets supplemented on occasion by deposit-feeding. The nervous system features long connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion and short cerebropedal connectives. Zygoneury is present.

Turritellids may be either gonochoristic or protandric hermaphrodites – the latter condition may in fact be typical of all uncoiled species (for example, *Vermicularia*). In females, a portion of the mantle cavity may be modified into a brood pouch (Morton, J.E. 1953b; Carrick 1980b). Males in some species may be substantially smaller than females (always so in protandric species) and are aphyallic. Recently, Kennedy (1995) demonstrated that at least in *Turritella communis*, structured spermatophores (Fig. 15.88I) are present, and are transferred from male to female via pseudocopulation (Fig. 15.88G). Euspermatozoa correspond to Healy's (1983) Group 1(i) (Afzelius & Dallai 1983; Koike 1985; Healy unpublished data); paraspermatozoa are of the basic cerithioid type (Melone, Lora Lamia Donin & Cotelli 1980; Healy 1986a, unpublished data). Uniquely among Cerithioidea, turritellid euspermatozoa are paired (Fig. 15.88H; Retzius 1906; Franzén 1955; Carrick 1980b; Afzelius & Dallai 1983; Bieler & Hadfield 1990; Kennedy 1995; Healy unpublished data). Eggs are grouped together in capsules enclosed in circular, transparent cases that form masses and are retained in the mantle cavity and brooded, or attached by strands to rocks, wood or other firm surfaces on the substratum (Bandel 1976a; Carrick 1980a, 1980b; Allmon 1988; Bieler & Hadfield 1990). In brooding species, the embryos may be released to a brief larval (dispersal) phase (Bieler & Hadfield 1990) or released as crawling juveniles (direct development – Iredale 1924; Carrick 1980a, 1980b). Eggs vary considerably in size, ranging from 100 µm in *Turritella communis* (Lebour 1933b) to 960–1000 µm in the Australian species, *Gazameda gunni* (Carrick 1980a, 1980b). Carrick (1980b) noted that brood number in *G. gunni* is larger in larger females, but that egg size appears to be constant in all females. The brooding time for eggs in *G. gunni* – 200 days according to Carrick (1980b) – appears to be one of the longest for any marine prosobranch. Brooding has also been reported for fossil turritellid species by a number of authors (see Marwick 1971; Antill 1974; Allmon 1988 and references therein).

Most published studies on turritellid anatomy and biology have centred on Atlantic species such as *Turritella communis* (Randles 1900; Graham 1938; Yonge 1946; Fretter & Graham 1962; Kennedy & Keegan 1992; Kennedy 1995) and the uncoiled *Vermicularia spirata* (Morton, J.E. 1953b; Gould 1969; Bieler & Hadfield 1990). There have, however, been a few studies on Indo-Pacific or West Pacific species such as *Turritella terebra* (from Hong Kong, Hickman 1985), *Maoricolpus roseus* (New Zealand and Tasmania, Allmon, Jones, Aiello, Gowlett-Holmes & Probert 1994) and *Gazameda gunni* (New South Wales, Carrick 1980a, 1980b). In addition, Allmon (1988) has presented an excellent review of turritelline (subfamilies Turritellinae + Protominae) biology, ecology and bathymetric and geographic distribution. He concluded that turritellines were much more ecologically and biologically diverse than early generalisations had suggested. They exhibit for example varying reproductive and developmental strategies (protandry or gonochorism; pelagic larvae or direct development), often wide tolerance to salinities and sediment type, often wide depth range, both suspension-feeding and deposit-feeding and, appeared to prefer cooler rather than warmer waters.

Graham (1938) and Yonge (1946) described feeding in *Turritella communis*. After burrowing into gravelly mud, the foot creates a depression in the substratum and subsequently shows little movement (Fig. 15.88F). Feeding involves the consumption of mucous ropes containing particles removed from the ctenidium by ciliary currents. There are two overlapping folds to the right side of the head which serve as an exhalant siphon, allowing water and faeces to be expelled from the mantle cavity without disturbing the surrounding sediment. A partially infaunal position is adopted by most turritellids on soft bottoms (with openings to the inhalant and exhalant channels maintained free of sediment) (Yonge 1946; Hickman 1985; Allmon 1988), and animals living on hard substrata (gravel, coarse shell grit bottoms) are usually epifaunal (Allmon 1988). According to Hickman (1985) the snout of the tropical species, *Turritella terebra*, plays an important role in maintaining a

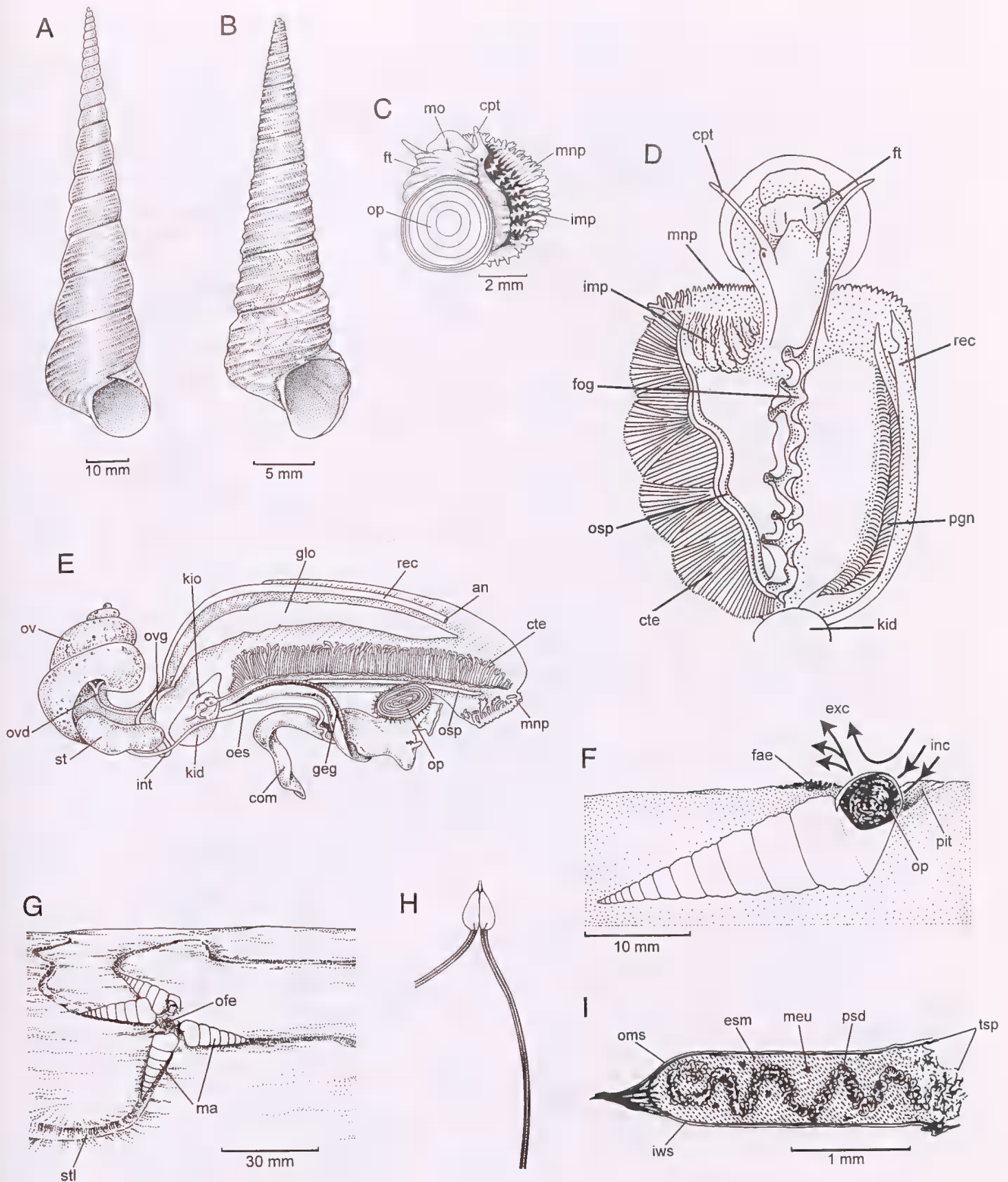


Figure 15.88 Family Turritellidae. **A, B**, shells, apertural view: **A**, *Turritella terebra*; **B**, *Colpospira runcinata*. **C**, *Turritella communis*, a partially retracted animal, ventral view, showing mantle papillae of the inhalant aperture to the mantle cavity. **D**, *Vermicularia spirata*, mantle cavity opened dorsally by an incision through the hypobranchial gland, showing the position of the pallial gonoduct in both sexes. **E**, *Turritella communis*, female, dissected to show the arrangement of the reproductive organs. **F, G**, *Turritella communis*, behaviour: **F**, typical position of quiescent individuals buried in the sediment during ciliary suspension-feeding at the sediment surface - arrows indicate local incurrent and excurrent water flow; **G**, males on the surface of the sediment engaged in pseudocopulatory behaviour - the buried ostensible female (ofe) is indicated. **H**, paired euspermatozoa of *Turritella* sp. **I**, spermatophore of *Turritella communis*. an, anus; com, columellar muscle; cpt, cephalic tentacle; cte, ctenidium; esm, euspermatozoal mass; exc, exhalant current; fae, deposited faecal pellets propelled from pseudo-siphonal process in the exhalant current; fog, food groove; ft, foot; geg, genital groove; glo, glandular portion of oviduct; imp, inner mantle papillae; inc, inhalant current; int, intestine; iws, inner gelatinous wall of spermatophore; kid, kidney; kio, kidney opening; ma, male animals; meu, morulae of paired euspermatozoa; mnp, mantle papillae; mo, mouth; oes, oesophagus; ofe, ostensible female animal; oms, outer membranous spermatophore covering; op, operculum; osp, osphradium; ov, ovary; ovd, oviduct; ovg, oviducal gland; pgn, pallial gonoduct; pit, pit created by inhalant feeding current; psd, diverticular membrane containing paraspermatozoa; rec, rectum; st, stomach; stl, surface trails left by males; tsp, torn end of spermatophore separated from the opercular bristles. (C, after Fretter & Graham 1962; D, after Bieler & Hadfield 1990; E, after Randles 1900; F, G, I, after Kennedy 1995; H, after Retzius 1906) [R. Plant]

physical barrier between the inhalant and exhalant siphonal apertures. In some populations of *Maoricolpus roseus* from New Zealand, the animals may be found on the sediment or, very commonly, wedged into crevices in rocks (Allmon *et al.* 1994).

The genus *Vermicularia*, with a partially uncoiled shell, was included in the Vermetidae until J.E. Morton (1953b) examined its anatomy and feeding mechanisms. He clearly demonstrated similarities between *Vermicularia* and *Turritella communis* in the morphology of the pallial tentacles, ctenidium, food groove and foot, radula, embryonic shell, development and operculum, and transferred *Vermicularia* to the Turritellidae (Morton, J.E. 1953b). The family was revised at the supraspecific level by Marwick (1957) who recognised five subfamilies – Turritellinae, Protominae, Pareorinae, Turritellopsinae, plus Habe's (1955) Orectospirinae – and 33 genera (one of uncertain affinities). A further subfamily, Vermiculariinae is currently reserved for the partly uncoiled genus *Vermicularia*. Cotton & Woods (1935) gave a brief overview of the Recent and fossil South Australian turritellids and Garrard (1972, 1982) revised all Recent Australian species and recognised about 40 extant valid species in 10 genera and three subfamilies (Turritellinae, Pareorinae, Turritellopsinae). Such numbers suggest that Australia may have one of the highest diversities of turritellids in the world. Certainly, Allmon (1988) has identified the New Zealand–Australian region as being an area of high turritelline density. The tendency towards a short planktonic stage and direct development is probably a contributing factor in the generation of high species diversity within the Turritellidae (Marwick 1957; Garrard 1972, 1982; Allmon 1988). The majority of the 27 living Australian species (20 of them endemic) belong to the genus *Colpospira* (subgenera *Colpospira*, *Acutospira*, *Ctenocolpus*, *Platycolpus*). Other diverse genera include *Archimediella* (four species, two endemic), *Gazameda* (four species, three endemic) and *Haustator* (three species, two endemic). Several taxa are illustrated in colour by Wilson (1993). Allan (1959) erroneously assigned some Australian vermetids (Vermetoidea) to *Vermicularia*.

The relationship of the family to other cerithioideans is still unclear. Houbbrick (1988) concluded from his cladistic analysis that turritellids are closely related to the Vermetidae and that these two families form the sister clade to the Potamididae + 'Cerithiidae' + Modulidae + Batillariidae. However, sperm ultrastructural studies have shown that the Vermetidae not only have no connection with the Turritellidae (or related Siliquariidae), but should be included in their own superfamily (Healy 1988b). Houbbrick considered the Turritellidae to be an old family and expressed surprise that they should emerge as a terminal group within his phylogeny. Using a revised set of Houbbrick's characters, and excluding the Vermetidae, Ponder (1991b) analysed cerithioidean phylogeny cladistically. His results suggested that the Turritellidae either emerged early (Campanilidae – his preferred outgroup) or last (Rissoidae as outgroup) in the tree. Comparative sperm ultrastructure suggests that the Turritellidae are more closely related to the Cerithiidae, Dialidae, Litiopidae and Siliquariidae than to other cerithioidean families (Healy 1983, 1986a). The relationship of the turritellid subfamily Orectospirinae to the rest of the family is dubious. The pagoda-like shell with its clearly marked anterior siphonal notch (Tsuchida 1966) suggests a possible connection with the Plesiotrochidae (Campaniloidea).

Turritellids extend back at least to the Late Cretaceous and there are many described fossil species (Marwick 1957; Allmon 1988). Allmon (1988) estimated that the combined number of named Recent species and subspecies of 'turritellines' (= subfamilies Turritellinae + Protominae) is approximately 500, with a further 1000 named extinct forms.

Several fossil turritellids are known from the Australian region – 24 valid species are listed by Garrard (1972). Turritellid fossils have also proved to be of considerable use in biostratigraphic correlation and age determination of sedimentary strata from the late Cainozoic of Japan, New Zealand, Italy and North America (Marwick 1957; Kotaka 1978).

Family Siliquariidae

The Siliquariidae are an unusual family of medium to large-sized marine cerithioideans which, like the turritellid genus *Vermicularia*, undergo a process of dextral uncoiling with continued growth (Gould 1966, 1969). The animals are suspension-feeders and live subtidally or sometimes intertidally in aggregations deep within sponges or among coralline algae in temperate to tropical regions (Morton, J.E. 1951c; Hughes, R.N. 1985a; Wilson 1993). Siliquariids can be distinguished from turritellids by the following features: teleoconch whorls inflated and showing no or minimal contact with each other; pallial tentacles usually absent; frequently a longitudinal slit in the teleoconch which may be closed off at intervals to form minute perforations; operculum with long, branching bristles. The family comprises a single genus, *Tenagodus* (= *Siliquaria*, see Bieler 1992b for discussion) which is divided into three subgenera: *Tenagodus sensu stricto* (shell slit continuous, protoconch conspiral, operculum conical), *Pyxipoma* (shell slit often discontinuous, closed off into a series of holes, protoconch planispiral, operculum conical), *Stephopoma* (shell slit absent, protoconch planispiral, operculum flat).

The shell is loosely (sometimes very loosely) coiled for the initial two to five whorls, but thereafter uncoils dextrally (Fig. 15.89A). An umbilicus is present, and the succeeding whorls, although sometimes spatially close to each other, show minimal points of physical contact. A continuous slit, often constricted at short intervals (1–3 mm) to form a series of holes, is commonly present on the middle dorsal surface of each whorl, and continues to the aperture – slit absent in *Tenagodus* (*Stephopoma*). After the first one to one and a half whorls, the sculpture consists of well-developed growth ridges, the defining edges of which correspond to the points of constriction of the shell slit. Sculpture in the uncoiled portion of the shell consists of broad and parallel longitudinal ridges crossed at irregular intervals by fissure-like transverse growth lines. In some species, spinose spiral cords may be present. The protoconch (Fig. 15.89F, G) is low-spined to almost nautiloid in appearance and consists of a smooth, initial half whorl followed by a finely to coarsely pustulose one and a half whorls. The operculum is conical or flat with prominent, peripheral bristles that are often branched (Fig. 15.89B; Morton, J.E. 1951c; Morton, J.E. & Keen 1960).

The following summary of siliquariid anatomy is based on studies of *Tenagodus* (*Pyxipoma*) and *T. (Stephopoma)* by J.E. Morton (1951c, 1953b), J.E. Morton & Keen (1960) and R.N. Hughes (1985a). The head-foot (Fig. 15.89B, C, D) features a short blunt snout; a pair of very short cephalic tentacles; a small eye situated on the outer base of each cephalic tentacle; a short foot with a ciliated groove on the right side, and a mobile, muscular, pre-oral appendage developed from the anterior portion of the foot. The entire mantle edge is ornamented with numerous small papillae. A long slit in the mantle occurs on the right side. In the mantle cavity (Fig. 15.89E) are an elongate, ridge-shaped (simple) osphradium (equal in length to the ctenidium); a long ctenidium with elongate filaments (involved in ciliary-mucous feeding); a well-developed hypobranchial gland (? lacking distal leaflets); rectum; renal organ; and gonoduct. Each tooth row of the radula (Fig. 15.89H, I) has a square central tooth with a large central cusp either flanked by several smaller cusps – *T. (Stephopoma)* – or lacking them – *T. (Pyxipoma)*. The lateral teeth are elongate-quadrate with only a terminal cusp – *T. (Stephopoma)* – or a terminal cusp with an outer smaller cusp – *T. (Pyxipoma)*, and the marginal teeth are scythe-like without cusps. Food collected by the ctenidium is conveyed by cilia first to the food groove on the floor of the mantle cavity, then along the groove to the mouth. The anterior portion of the foot is developed into a papilliform pre-oral appendage (Fig. 15.89D). This appendage assists in moving the food-containing mucous rope from the food groove to the mouth where the radula grips the mucous rope. The oesophagus leads to a small triangular or crescentic stomach featuring a style sac, a small crystalline style and a small gastric shield. The structure of the nervous system in siliquariids has not yet been examined. Presumably it is similar in organisation to that of the Turritellidae.

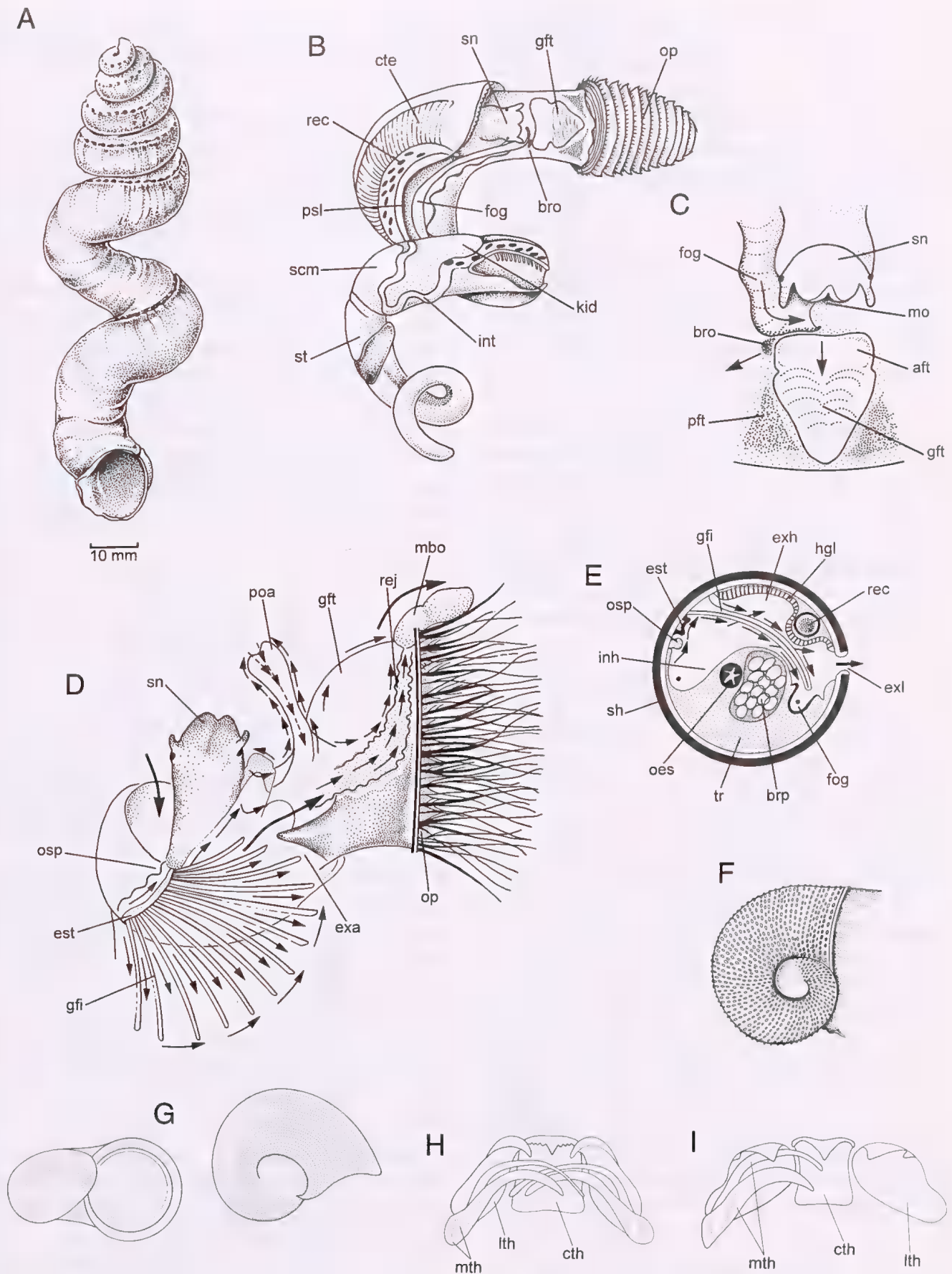


Figure 15.89 Family Siliquariidae. **A**, *Tenagodus (Tenagodus) australis*, shell. **B**, **C**, *Tenagodus (Pyxipoma) weldii*: **B**, animal, right lateral view, showing external body features and the conical operculum; **C**, head and foot, showing the relationship of head, food groove and anterior marginal flap of foot. **D**, *Tenagodus (Stephopoma) roseum*, head and foot region of a fully extended animal, showing the pre-oral appendage of the foot, the ctenidial sweeping fringe and the course of the feeding and retractor currents. **E**, *Tenagodus (Pyxipoma) sp.*, diagrammatic transverse section of the mantle cavity; arrows show the direction of the principal ciliary currents. **F**, *Tenagodus (Stephopoma) nucleogranosum*, protoconch attached to the teleoconch. **G**, *Tenagodus (Pyxipoma) weldii*, protoconch, apertural (left) and apical (right) views. **H**, **I**, portions of radula: **H**, *Tenagodus (Stephopoma) roseum*, a transverse radular tooth row; **I**, *Tenagodus (Pyxipoma) weldii*, part of a transverse radular tooth row. **aft**, anterior portion of foot; **bro**, opening of brood pouch; **brp**, brood pouch; **cte**, ctenidium; **cth**, central tooth; **est**, endostyle; **exa**, exhalant siphonal appendage; **exh**, exhalant chamber; **exl**, exhalant slit; **fog**, food groove; **gfi**, gill filament with tract of lateral cilia; **gft**, glandular region of foot; **hgl**, hypobranchial gland; **inh**, inhalant chamber of mantle cavity; **int**, intestine; **kid**, kidney; **lth**, lateral tooth; **mbo**, mucus bolus; **mth**, marginal teeth; **oes**, oesophagus; **op**, operculum; **osp**, osphradium; **pft**, pigmented lateral region of foot; **poa**, pre-oral appendage; **psl**, pallial slit; **rec**, rectum; **rej**, retractor tract of foot; **scm**, style caecum; **sh**, shell; **sn**, snout; **st**, stomach; **tr**, muscular region of trunk. (**B**–**D**, **F**–**I**, after Morton, J.E. 1951c; **E**, after Morton, J.E. 1955a) [A, R. Plant; **B**–**I**, A.J. Hill]

15. PROSOBRANCHS

Although J.E. Morton (1951c) described the basic features of the male and female reproductive systems of *Tenagodus* (*Stephopoma*) *roseum* and *T. (Pyxipoma) weldii*, it is not known whether siliquariids may in fact be protandric hermaphrodites (Morton, J.E. did not give any indication of male and female size). In *Tenagodus* (*Tenagodus*) *cumingii*, testis tissue has been observed only in small individuals (Healy unpublished data), suggesting the possibility of protandry in this species. Females have albumen and capsule glands. Siliquariids are brooders; they retain developing embryos either freely within the mantle cavity or in a special brood pouch developed from the head-foot (the pouch opening on right side of head-foot; Fig. 15.89E). Brood numbers vary from 10 to 15 in *T. (Stephopoma) roseum* to 100 to 150 in *T. (Pyxipoma) weldii* (Morton, J.E. 1951c), the number in *T. (Pyxipoma)* being much smaller than in *T. (Stephopoma)*. Duration of the brooding process is unknown. Males are usually aphyallic, but R.N. Hughes (1985a) has described and illustrated the presence of a 'tentaculiform penis' in the Panamanian species *T. (Stephopoma) pennatum*. R.N. Hughes observed sperm being ejected in a stream from the penis of one individual and sucked into the inhalant aperture of a neighbouring individual (8 mm distant). J.E. Morton (1951c) suggested that sperm transfer in *T. (Stephopoma) roseum* was probably effected by ciliary-induced exhalant and inhalant currents. Given that sperm are packaged in spermatophores in most cerithioideans (Houbrick 1988) and that these structures have only recently been detected in the related Turritellidae (Kennedy 1995), it seems likely that siliquariids may also produce spermatophores. Spermatozoa are probably dimorphic as in other cerithioideans. Ultrastructural examination of formalin-preserved testis material of *Tenagodus* (*Tenagodus*) *cumingii* (Healy unpublished data) indicates that euspermatozoa are of Group 1(i) of Healy (1983).

Although briefly described in popular books (for example, Allan 1959; Macpherson & Gabriel 1962; Wilson 1993) and listed in various regional checklists (May 1923; Iredale & McMichael 1962), there have been no biological or ecological studies of siliquariids in Australia. Wilson (1993) lists four siliquariid species from Australian waters – three belonging to *Tenagodus* (listed as *Siliquaria*) (the Indo-West Pacific species *Tenagodus anguina* and *T. ponderosa*, and endemic *T. australis*) and one belonging to *Tenagodus* (*Pyxipoma*) [*T. (Pyxipoma) weldii*, recorded from Australia and New Zealand]. *Tenagodus* and *Pyxipoma* were treated by Wilson as subgenera of *Tenagodus sensu lato*. Two species of *T. (Stephopoma)* are also recorded from Australia – *T. (Stephopoma) nucleogranosum* and *T. (Stephopoma) tricuspe* – (Morton, J.E. 1951c; Iredale & McMichael 1962). Unfortunately, the Australian siliquariids have never been reviewed, hence it is impossible at the present time to give any estimate of the number of valid species in the fauna. The Indo-West Pacific species, *Tenagodus* (*Tenagodus*) *ponderosa*, which occurs in tropical northern Australia is the largest living siliquariid and probably also the largest living cerithioidean, reaching lengths in excess of 450 mm (size range from 125–467 mm according to Eisenberg 1981). Macpherson & Gabriel (1962) noted that colonies of *T. (T.) australis* (embedded in sponges) measuring up to 1800 mm x 300 mm have been trawled from Bass Strait; whereas *T. (Pyxipoma) weldii* living at a depth of 14 m off Phillip and French Islands forms much smaller sponge-embedded colonies commonly reaching 150–200 mm in diameter.

Unquestionably, the closest relationship of the Siliquariidae with other cerithioideans is with the Turritellidae (Morton, J.E. 1953b) one subfamily of which – the Vermiculariinae – also shows uncoiling of the shell. Whether or not the Siliquariidae can be retained as a separate family is problematic, some authors preferring to incorporate the group within the Turritellidae (in the subfamily Vermiculariinae – Abbott 1974; Hughes, R.N. 1985a). J.E. Morton (1951b, 1951c, 1951d) in a series of detailed papers, demonstrated that siliquariids are a separate group from the Vermetidae. Houbrick (1988) did not include the Siliquariidae in his analysis of cerithioideans because of the lack of data on the family.

The only fossil record of the Siliquariidae from Australia is that of Ludbrook (1984) who noted a single specimen of *T. (Pyxipoma) weldii* (as *Siliquaria weldii*) from the Late Pleistocene Glanville Formation of South Australia.

Family Batillariidae

The Batillariidae, although not large in terms of numbers of species, is well represented in the Indo-West Pacific where certain species of *Batillaria* may dominate temperate to tropical estuarine mudflats (Ewers 1963; Wells 1984). Despite their obvious ecological importance the Batillariidae have never been monographed.

The Batillariidae were traditionally included in the Potamididae as a subfamily (for example, Thiele 1929–1935) until Healy (1983) and Houbrick (1988) recommended the establishment of a separate family, a suggestion followed by Ponder & Warén (1988) in their listing of cerithioidean families. Features that separate the Batillariidae from the Potamididae include sperm differences (euspermatozoa with midpiece of Group 1(ii) type; paraspermatozoa with fewer flagella and nuclear core not penetrating into the base of the acrosome-like structure – Healy 1983, 1986a); presence of lateral denticles on the basal plate of the central tooth; and the morphology of the sperm gutters in the female. In addition potamidids do not range into temperate regions, whereas batillariids may be particularly common there.

The batillariid shell is turreted, many whorled (whorls convex), often narrow and usually has heavy axial and spiral sculpture in the form of ridges and/or blunt nodules (Fig. 15.90A–C). Mature and gerontic shells can be very corroded or smooth because of exposure to acidic mud and/or mineral deposition. The aperture shows an anterior siphonal notch and typically is weakly flared in mature specimens of most genera, but moderately to strongly flared in *Pyrazus*. Mature shells range in size from very small (3 mm – *Batillariella estuarina*) to large (up to 100 mm in *Pyrazus ebeninus*). Teleoconch colour ranges from black to brown-grey, with *Batillaria* also producing white-banded specimens (Ewers & Rose 1966a, 1966b; Ewers 1967a; Wells 1985). Features of the protoconch have not yet been described. The periostracum is thin or thick, and the operculum is corneous, multispiral with a central nucleus (Fig. 15.90D).

The following anatomical summary is based on several sources including MacIntyre (1961), Driscoll (1972), Healy & Jamieson (1981) and Houbrick (1988). The head-foot features a short, wide snout; a pair of long cephalic tentacles each with an eye situated near the tentacle base; a short broad foot with a ciliated groove on the right side. The upper mantle edge has a few short papillae and, in *Pyrazus ebeninus*, is equipped with pallial eye-like structures (Tenison Woods 1888). Within the mantle cavity are a thin, ridge-shaped (simple) osphradium, a ctenidium with long filaments, a well-developed hypobranchial gland, a renal organ, the rectum and gonoduct. Each tooth row of the radula (Fig. 15.90H) has a quadrate to trapezoidal central tooth with a long central cusp (Fig. 15.90G) flanked by one or more smaller cusps, and a basal plate with a pair of laterally placed denticles and often a pair of lateral extensions. The lateral teeth have a long, narrow shaft and a large cusp flanked on the inner side by a small cusp and on the outer side by four or more small cusps. The marginal teeth are terminally curved with multiple small cusps. The alimentary tract and buccal cavity are illustrated in Figure 15.90F and 15.90E respectively. The salivary glands are paired and each is composed of three to four small convoluted tubules (Fig. 15.90E, F). These glands pass through the nerve ring before opening into the buccal cavity. Ciliated ridges within the stomach assist in sorting of food and sediment (batillariids usually are deposit-feeders). The stomach features a moderately large style sac containing a crystalline style (Driscoll 1972). The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion and long cerebropedal connectives. Zygoneury is present. Batillariids are dioecious. Females are characterised by having sperm gutters on

both laminae of the pallial oviduct (Houbrick 1988). Euspermatozoa correspond with Group 1(ii) type of Healy 1983; paraspermatozoa are of the basic cerithioidean type (Healy & Jamieson 1981; Healy 1982b, 1983, 1986a). MacIntyre (1961) noted that eggs of aquarium-held *Batillaria australis* (from New South Wales) are opaque and white, and are laid during summer (late February) in a thin, transparent tubular string consisting of fine, zig-zag waves 2 mm in width. According to MacIntyre, an eight-celled blastula stage is reached seven hours after egg deposition. Within 24 hours the trochophore is complete and after 48 hours the veliger (showing operculum, shell, eyes and statocysts) is actively swimming within the egg capsule. Hatching of *B. australis* eggs occurred after 60 hours. Gametogenesis in this species begins in the spring for animals over 17 months in age, and the life span of adult specimens is estimated to be between two and one half to four years (Appleton 1980).

Australian batillariids are essentially temperate to subtropical in distribution with some species such as *Batillaria australis* and *Pyrazus ebeninus* ranging from Cape York (northern Queensland) southwards along the New South Wales coast to Victoria and Tasmania, with isolated, possibly introduced (Cotton 1959b; Wells & Bryce 1988) populations occurring in southern Western Australia (Swan River and Cockburn Sound, near the river mouth). Batillariids inhabit intertidal sandy-mudflats, coastal lakes and estuaries where their population densities may be extremely high; up to 200 per 30 cm² in New South Wales populations of *B. australis* according to Ewers (1963), and up to 360 to 393 per m² in populations of *Zeacumantus diemenensis* and

Batillariella estuarina from Albany, Western Australia (Wells & Roberts 1980). Four genera are usually listed as occurring in Australia: *Batillaria* (*B. australis*, endemic), *Pyrazus* (*P. ebeninus*, endemic and the largest of all batillariids), *Zeacumantus* (*Z. diemenensis*, endemic; *Z. subcarinatus*, introduced from New Zealand), and *Batillariella* (*B. estuarina*, endemic). The genus name *Velacumantus* although widely used in the Australian literature is now regarded as a synonym of *Batillaria* (Ludbrook 1984; W.F. Ponder personal communication). The genus name *Pyrazus* has been applied to various cerithioideans (living and fossil) other than *P. ebeninus*, but currently is used only for this species. Although mature shells of *Pyrazus ebeninus* are easily distinguished from those of *Batillaria australis* (with which it is commonly sympatric), juveniles of these two species can only be separated by small differences in basal sculpture (Ewers & Rose 1966a). The Pleistocene extinction in South Australian waters of *B. australis* may be connected with sea level changes as suggested by Ludbrook (1984), but may also be the result of high air temperature (Ewers 1967b). Two smaller endemic batillariids, *Zeacumantus diemenensis* and *Batillariella estuarina* are abundant and ecologically important in shallow, sandy areas on the south coast of the continent. Batillariids are also of biological interest because they act as the intermediate host for various trematode parasites of sea birds. The most significant of these is *Austrobilharzia terrigalensis*, a schistosome, which in its cercarial stage, burrows unsuccessfully into the skin of bathers causing the condition known as 'swimmer's itch' or 'schistosome dermatitis' (Bearup 1955, 1956; Pope 1955). Apart from this aspect, little is known of the ecology or biology of Australian batillariids.

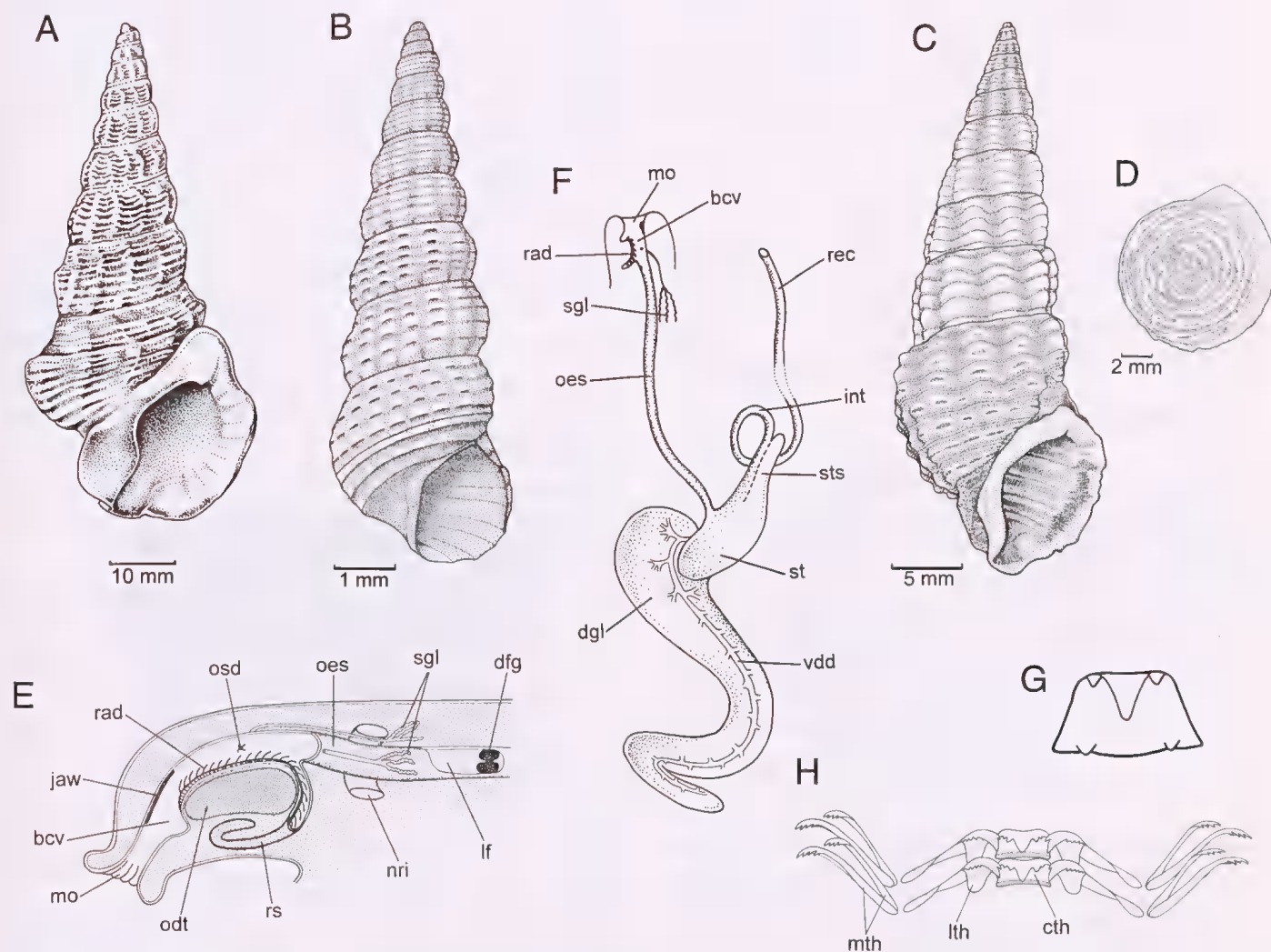


Figure 15.90 Family Batillariidae. A–C, shells, apertural view: A, *Pyrazus ebeninus*; B, *Batillaria estuarina*; C, *Batillaria australis*. D, *Pyrazus ebeninus*, operculum. E, *Batillaria zonalis*, buccal region, diagrammatic longitudinal section showing the inside of the buccal cavity and a portion of the oesophagus. F, *Batillaria zonalis*, alimentary tract. G, *Batillaria estuarina*, central tooth of radula. H, *Pyrazus ebeninus*, two transverse rows of radular teeth. bcv, buccal cavity; cth, central tooth; dfg, dorsal food groove; dgl, digestive gland; int, intestine; jaw, jaw; lf, lateral fold; lth, lateral tooth; mo, mouth; mth, marginal teeth; nri, nerve ring; odt, odontophore; oes, oesophagus; osd, opening of salivary gland duct; rad, radula; rec, rectum; rs, radular sac; sgl, salivary gland; st, stomach; sts, style sac; vdd, ventral duct of digestive gland. (E, F, after Driscoll 1972; G, after Thiele 1929–1935; H, after Hedley 1905)

[A, R. Plant; B–D, C. Eadie; E–H, A.J. Hill]

The geographic range, selection pressures and shell-colour polymorphism of both living and fossil *Batillaria australis* were studied in a series of papers by Ewers (1966, 1967a, 1967b, 1967c) and Ewers & Rose (1965, 1966b). These studies indicated that colour-banded *B. australis*, although more often subjected to fish predation, are also more resistant to trematode infections, thereby perhaps ensuring that any population will retain at least some breeding individuals during periods of massive infection (badly infected adult snails are effectively rendered sterile). Sperm ultrastructure of various Australian batillariids has been studied by Healy (1982b, 1983, 1986a), and Healy & Jamieson (1981), and MacIntyre (1961) and Appleton (1980) have provided some details of reproductive biology, larval development and aspects of parasite load. Vohra (1965) studied the ecology and biology of *Pyrasus ebeninus* showing that these snails are capable of withstanding long periods out of water and a great range of temperature and salinity variations. Like other large mangrove snails, *Pyrasus ebeninus* featured in the diet of east coast Aboriginal Australians, notably in Moreton Bay, where shells of this species form a major constituent of middens on the Bay islands. Shells of this species were also among those collected by Captain Cook in Botany Bay, and subsequently conveyed back to Europe for description (see Hedley 1905 for a summary of the nomenclatural history). McClatchie (1979) found that New Zealand *Zeacumantus subcarinatus* feeds primarily on the alga *Ulva lactuca*. This batillariid has been introduced into the Sydney area, New South Wales, probably by via shipping (in ballast water) from New Zealand (Powell 1979). Accidental introduction is also probably responsible for the spread of *Batillaria australis* to Western Australia. Wells (1985) found that although two species of *Batillaria* occur in a single mangal system in Hong Kong, they occupy different habitats. Driscoll (1972) has shown that *Batillaria zonalis* in California is a deposit-feeder. Yamada (1982) demonstrated that this species has a relatively predictable recruitment level and a life span of 6–10 years in British Columbia.

Ludbrook (1984) recorded the extant *Zeacumantus diemenensis* and *Batillariella estuarina* and the extinct *Zeacumantus bivaricata* from the Quaternary of South Australia. She noted that *Z. diemenensis* also occurs in the Late Pliocene of South Australia. *Batillaria australis* occurs in Pleistocene deposits of South and Western Australia. Empty shells of this species and *Pyrasus ebeninus* from Lord Howe Island are probably also fossils (Brazier 1889; Iredale & Allan 1940).

Family Planaxidae

The Planaxidae are a small family of cerithioideans with only about 22 species worldwide, divided between two subfamilies Planaxinae and Fossarinae. The animals are mostly marine, being common on rocky intertidal shores in the tropics and subtropics. Their intertidal habitats on rocky shores (clustering under rocks in small recesses) are similar to those of many littorinids, although planaxids tend to be photonegative. Their compact shells are somewhat similar to those of littorinids, but planaxids can be distinguished by several anatomical features (such as open pallial ducts, aphillic males, cerithioid type euspermatozoa and multiflagellate paraspermatozoa) that clearly mark them as cerithioideans. In addition, the Planaxinae have a wide, shallow anterior canal in the shell aperture that is lacking in littorinids (Houbrick 1987a, 1988).

Houbrick (1987a) revised the Planaxinae and recognised 20 species distributed between the genera *Hinea*, *Planaxis*, *Fissilabia*, *Angiola*, *Supplanaxis* and *Holcostoma*. He subsequently added a further genus, *Simulathena*, containing only one New Guinean species (Houbrick 1992b). Ponder (1988b) concluded that *Angiola* is indistinguishable from *Hinea*; both have been shown to exhibit bioluminescence. The Fossarinae comprises *Fossarus*, which is sometimes placed within in its own family, the Fossaridae, and has in the past been included in a number of different superfamilies including the Hipponicoidea, Calyptraeidea and Littorinoidea.

Ponder (1980a) considered that the genus belongs in the Cerithioidea on the basis of its open pallial gonoducts and aphillic males. He also suggested that the presence of cephalic brood pouches in *Fossarus* and Planaxidae indicates a close relationship between the two groups. Houbrick (1990a) investigated the biology, anatomy and systematics of *F. ambiguus* in the Portuguese Azores and included the Fossaridae as a subfamily of the Planaxidae. He listed the following five features as diagnostic of the subfamily Fossarinae (Fig. 15.91A, D): a turbinate shell with a large, umbilicate body whorl and strong spiral cord sculpture; a heavily ciliated cephalic hood; a wide ciliated strip on the dorsal surface of each cephalic tentacle; the nervous system tightly organised with very short supra-oesophageal connectives; presence of dwarf males; and possible protandry.

In Planaxidae, the shell is small or moderately small in size (5–25 mm; Fig. 15.91A, D), and either conical and lacking a true umbilicus (Planaxinae) or turbinate and umbilicate (Fossarinae). The aperture is always wide and oval to round in profile. Whereas in the Planaxinae the outer lip is thickened (sometimes lirated) and shows an anterior siphonal notch, in the Fossarinae the lip is relatively thin and shows no or little evidence of an anterior notch. Spiral sculpture is usually present and often strongly developed. The planaxine protoconch I is smooth or microscopically pustulate and shows one to one and a half whorls; protoconch II typically shows two whorls, a small number of spiral cords or striae and a well-developed sinusigeral notch (Fig. 15.91C; see Houbrick 1987a). In *Fossarus* species, (Houbrick 1990a) protoconch I consists of one unsculptured (but microscopically pitted) whorl and a two-whorled protoconch II stage which has cancellate sculpture and a deep sinusigeral notch. Periostracum may be very thick or thin and poorly developed (often eroded from the shell surface). The operculum is corneous, ovoid and paucispiral with a terminal or subterminal nucleus (Fig. 15.91B). Adult shells may be sexually dimorphic in size, with females larger; in Fossarinae, male dwarfism suggests the possibility of protandrous hermaphroditism (Houbrick 1990a).

The following summary of anatomical features is based on the work of Houbrick (Planaxinae – 1987a, 1988; Fossarinae – 1990a). The head-foot has a moderately long and extensible snout, long cephalic tentacles each with an eye at its base, an anterior pedal gland and a cephalic brood pouch (Fig. 15.91E–G). *Fossarus* also has two small lobes between the cephalic tentacles which form a ‘cephalic hood’ and a ciliary tract on the dorsal surface of the cephalic tentacles (Fig. 15.91G). The mantle edge is fringed by many papillae positioned on the top half of the mantle. The mantle cavity (Fig. 15.91E, G) contains a long, ridge-shaped osphradium; a long ctenidium with long filaments; a well-developed hypobranchial gland; a renal organ; the rectum; and gonoduct. Animals graze on microalgae on rocks. Each tooth row of the radula (Fig. 15.91H) has a trapezoidal central tooth with a large central cusp that may or may not be flanked on each side by small cusps, or, as in *Fossarus*, the central cusp may have eight or nine serrations on each side. The basal plate of the central tooth has a flat to convex basal edge, a pair of lateral denticles and a pair of lateral projections. The rhomboidal or sometimes rod-shaped lateral teeth have a cutting edge with one or more small inner cusps, a large main cusp and two or three, or sometimes, as in *Fossarus*, many small outer cusps. The inner and outer marginal teeth both have a large outer cusp and two smaller inner cusps. The pair of salivary glands passes through the nerve ring. An oesophageal gland is present. The stomach is associated with a short style sac and a crystalline style and gastric shield. The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion well separated from the pleural ganglion, extensions of the pedal ganglia and long cerebropedal connectives. Zygoneury is absent. Sexes are separate, but in *Fossarus ambiguus* only the smallest animals (0.4–0.8 mm) were found by Houbrick (1990a) to be males (suggesting to him the possibility of protandry). Pallial gonoducts are open in both sexes. The female system has a spermatophoral bursa, a seminal receptacle and glandular epithelium that probably

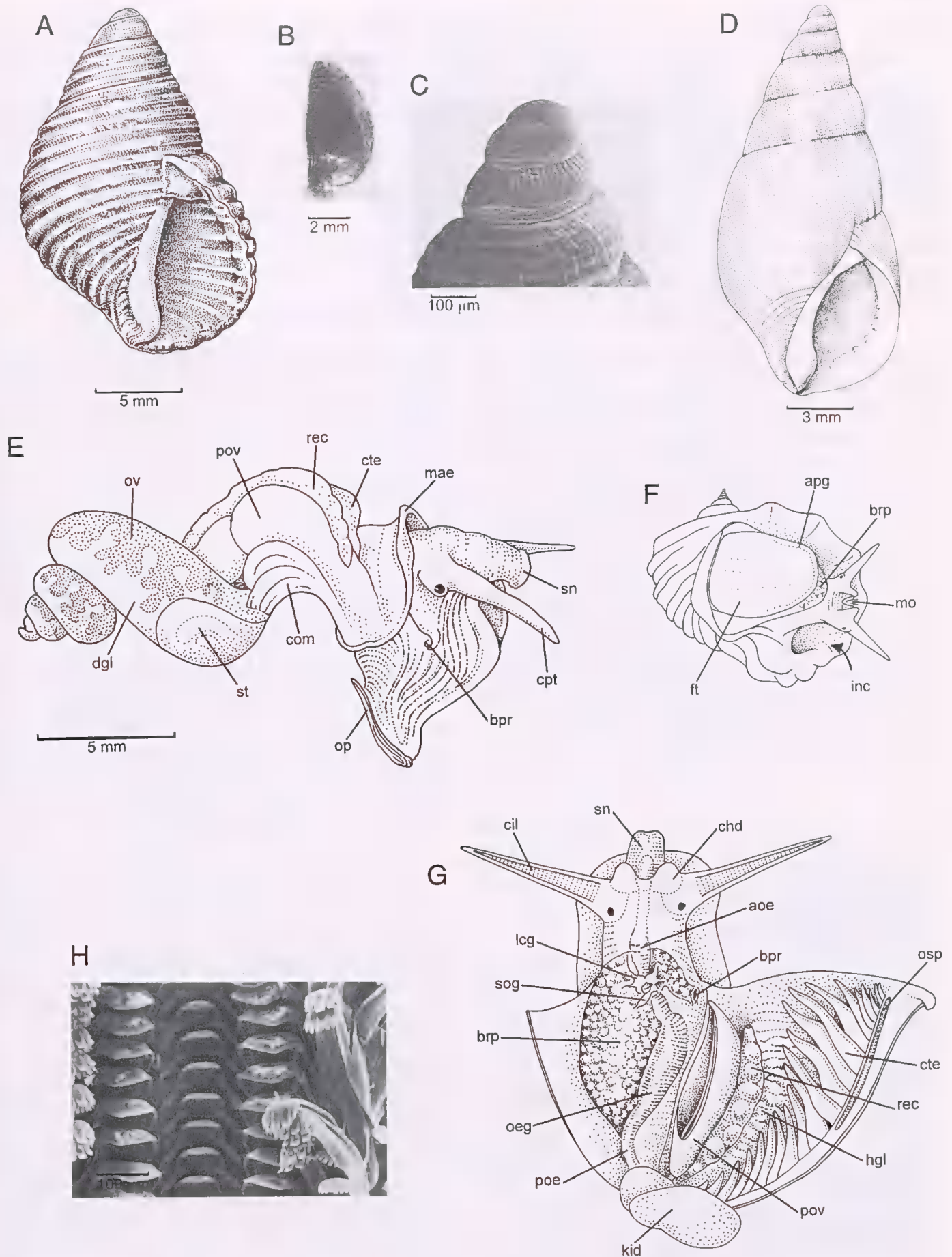


Figure 15.91 Family Planaxidae. **A–C**, *Planaxis sulcatus*: **A**, shell, apertural view; **B**, operculum, outer surface; **C**, protoconch and apical whorls of teleoconch. **D**, *Hinea brasiliiana*, shell, apertural view. **E**, *Planaxis sulcatus*, female removed from shell, right lateral view. **F, G**, *Fossarus ambiguus*: **F**, female withdrawn into its shell; **G**, dissection of female showing position of the mantle organs and the cephalic brood pouch. **H**, *Planaxis sulcatus*, several transverse rows of the radula, showing central, lateral and some marginal teeth. **aoe**, anterior oesophagus; **apg**, anterior pedal gland; **brp**, brood pore; **brp**, brood pouch; **chd**, ciliated cephalic hood; **cil**, ciliated strip on dorsal surface of cephalic tentacle; **com**, columellar muscle; **cpt**, cephalic tentacle; **cte**, ctenidium; **dgl**, digestive gland; **ft**, foot; **hgl**, hypobranchial gland; **inc**, inhalant current; **kid**, kidney; **lcg**, left cerebral ganglion; **mae**, mantle edge; **mo**, mouth; **oeg**, oesophageal gland; **op**, operculum; **osp**, osphradium; **ov**, ovary; **poe**, posterior oesophagus; **pov**, pallial oviduct; **rec**, rectum; **sn**, snout; **sog**, supra-oesophageal ganglion; **st**, stomach. (**B, C, H**, from Houbbrick 1987a; **E**, after Houbbrick 1987a; **F, G**, after Houbbrick 1990a)

[**A, D–G**, R. Plant]

functions as an albumen gland. Males are aphilic and produce spermatophores. Spermatozoa are dimorphic in the Planaxinae – the euspermatozoa being of the cerithioid type and belonging to Group 1(ii) of Healy (1983) (with Batillariidae); the paraspermatozoa have an acrosome-like structure, a condensed nuclear core surrounded by dense vesicles, midpiece and multiple flagella (most similar to those of Cerithiidae and Batillariidae) (Healy 1986a). Houbbrick (1990a) could only find euspermatozoa in *Fossarus ambiguus*, and unfortunately no ultrastructural information is available to confirm the cerithioidean nature of these cells. In *Fossarus*, embryos (each contained in a clear capsule) are retained within the cephalic brood pouch until the veliger stage, after which they emerge from their capsules and become free-swimming. In the Planaxinae, embryos may be released as free-swimming larvae or be retained until hatching; both strategies may occur in the same genus.

Claims made by some authors (for example, Thorson 1940; Morrison 1954; Barkati & Ahmed 1982) that planaxids are parthenogenetic were shown by Houbbrick (1987a) to have no basis; all investigated genera are dioecious. Possibly these reports reflect a misinterpretation of the significance of the brood pouch which also occurs in the Thiariidae (Thiariinae) – a group well known to be largely parthenogenetic (Houbbrick 1988). The wide aperture of planaxid shells undoubtedly assists in accommodating the cephalic brood pouch when it is filled with embryos. Sperm ultrastructure in the Fossarinae has not yet been investigated, but curiously Houbbrick (1990a) could only find euspermatozoa in *Fossarus ambiguus* (possibly due to seasonal absence of paraspermatozoa). All planaxids that have been studied protect their developing young in cephalic brood pouches, usually until they are released as veligers (Houbbrick 1987a). The stage reached by the young at the time of release varies in the different species, as do the number of embryos brooded and the morphology of the brood pouch (simple pouch in *Hinea*, complex pouch present in *Planaxis* – see Houbbrick 1987a for details). Some species such as the abundant Indo-Pacific species *Planaxis sulcatus* may have embryos representing multiple brooding cycles (see Houbbrick 1987a).

Several species of *Hinea* are unusual among gastropods in that they have a luminescent mantle organ of unknown function (Haneda 1958; Houbbrick 1987a; Ponder 1988b). Ponder (1988b) recorded that *Hinea brasiliana*, from New South Wales, emits a bright blue-white light when disturbed, usually for a few seconds but for up to a minute in one instance.

Three planaxine genera, *Planaxis*, *Fissilabia*, and *Hinea* have been recorded from Australian waters (Houbbrick 1987a) and two fossarine species (in *Fossarus*) were listed by Wilson (1993). The most widely distributed species is *Planaxis sulcatus*, which occurs on rocky intertidal shores across northern Australia from Western Australia to southern Queensland and, in fact, throughout much of the Indo-West Pacific (Houbbrick 1987a). Houbbrick (1987a) has, however, suggested that because of reports of direct development in north-western Indian Ocean populations of this species (versus indirect development in Pacific populations) it is possible that '*Planaxis sulcatus*' may comprise at least two cryptic species. Genera differ in their preferred position on the shore: *Hinea* species occur much higher in the littoral zone than those of *Planaxis*, although some species of the latter can also inhabit very high positions. Rohde (1981) has examined the population dynamics and incidence of trematode infection of *P. sulcatus* at Heron Island on the Great Barrier Reef and found that this species acts as an intermediate host for a number of trematodes, including *Austrobilharzia terrigalensis* which is responsible for 'swimmer's itch'. *Hinea brasiliana* is widely distributed in southern Australia and also occurs at Norfolk Island, Lord Howe Island, the Kermadec Group and northern New Zealand (see Houbbrick 1987a). *Fissilabia decollata* lives high in the intertidal zone in northern Queensland.

The planaxid fossil record is sparse, and although Houbbrick (1987a) listed material from the Eocene (Europe and Egypt) and Pliocene (Jamaica, Venezuela and Java) he could find no records from Australia. The family may have had its origins in the Cretaceous if Egyptian material is truly referable to *Planaxis* (Mahmoud 1956). Sperm ultrastructure (Healy 1983, 1986a) and central tooth structure suggest a link with the Batillariidae, although the presence of a brood pouch also points to possible thiarid links (Houbbrick 1987a). Good comparative sperm data for thiarids may greatly assist in resolving planaxid relationships. Houbbrick's cladistic analysis indicates two clades within the Planaxinae (including '*Angiola*'): *Fissilabia* + *Planaxis* and *Supplanaxis* + *Hinea*.

Family Potamididae

The Potamididae are an ecologically important family of medium- to large-sized cerithioideans inhabiting mangroves and estuarine mudflats throughout tropical and subtropical regions of the world (see Pl. 24.2; Wells 1980a, 1985; Houbbrick 1984c, 1986b, 1988, 1991). Potamidids have turreted, highly sculptured shells ranging in length from 20–100 mm (some species reaching up to 190 mm), a taenioglossate radula, and are detritivores. The Potamididae *sensu stricto* are distinguished from other cerithioideans by having small mantle papillae and a small radula with a narrow basal plate on the central teeth. They are most likely to be confused with members of the mangrove-estuarine family Batillariidae which, like the Potamididae also have a round, multispiral operculum. However, the central teeth of the batillariid radula differ from those of potamidids in having lateral denticles and often lateral extensions on the basal plate.

Traditionally, the Potamididae have been subdivided into two subfamilies, the Potamidineae and Batillariinae (Thiele 1929–1935). However, appreciation of anatomical, sperm ultrastructural and electrophoretic differences between these groups has resulted in recognition of a separate family, the Batillariidae (for data see Bishop 1979; Healy 1983; Houbbrick 1988). Houbbrick (1988) also created a new family for the potamidid genus *Cerithidea* (Cerithideidae), but subsequently (1991) returned it to the Potamididae.

Houbbrick (1984c) undertook a cladistic analysis of *Cerithidea sensu lato* based on comparative shell, radular and anatomical features, and found support for recognition of three subgenera – *Cerithidea sensu stricto*, *Cerithiopsis* and *Cerithiopsilla*. He later concluded (Houbbrick 1991) that the genus is closely related to *Telescopium* and *Terebralia*, showing similarities in the alimentary system and mantle cavity and the presence of a pallial eye, but differs from these two genera by having two seminal receptacles.

The shells are elongate, multi-whorled and turreted, and sculptured with strong spiral ridges crossed typically with heavy axial ridges (Fig. 15.92A–C). They vary in thickness from thin (some species of *Cerithidea*) to very thick (*Telescopium*), and may be heavily corroded by environmental acids and/or coated with precipitated mineral deposits. Helical columellar and/or palatal plaits occur in *Telescopium* and *Terebralia*. The aperture is ovate to angular, usually with some degree of flaring of the outer lips and always with a short but clearly marked anterior siphonal canal. Shells range in size from relatively small (20 mm) to large (100 mm up to a maximum of 190 mm). Shell colour ranges from light brown to black and *Cerithidea* species sometimes feature spiral brown bands. Protoconch features are unknown for most species. In *Cerithidea scalariformis* (a direct developer), the protoconch is smooth, and bulbous with a smooth outer lip and consists of one and a half whorls (Houbbrick 1984c). The periostracum ranges from very thin to thick (often eroded due to environmental acids), and the operculum is corneous and multispiral with a central nucleus (Fig. 15.92D).

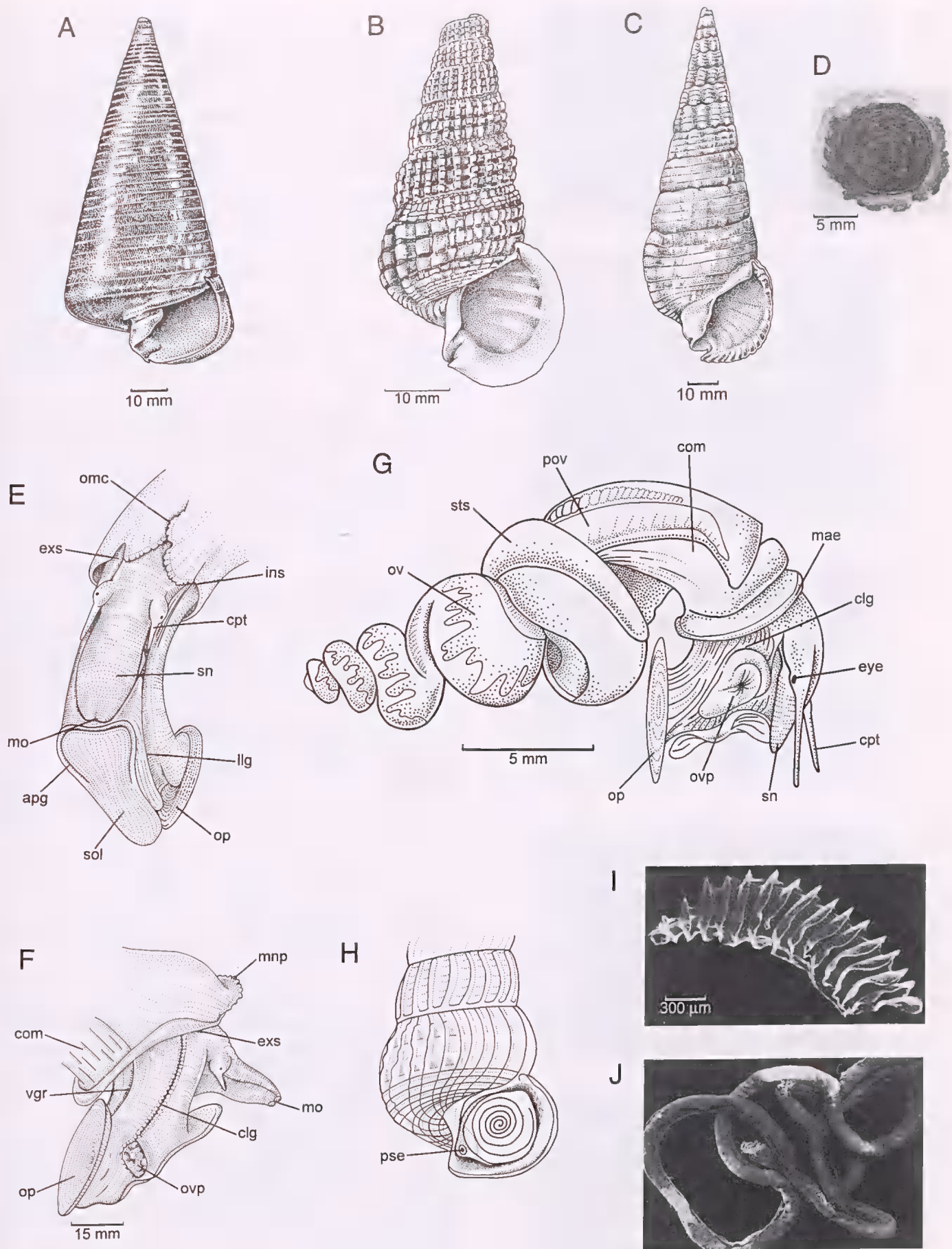


Figure 15.92 Family Potamididae. A–C, shells, apertural view: A, *Telescopium telescopium*; B, *Cerithidea reidi*; C, *Terebralia palustris*. D, *Terebralia palustris*, operculum, outer surface. E, F, *Telescopium telescopium*, anatomical features: E, head-foot, anterior view showing mantle edge, head and sole of foot, and the opening of the anterior pedal gland along the edge of foot; F, female, right lateral view, showing the ciliated groove and ovipositor. G, *Cerithidea californica*, female removed from shell, right lateral view. H, *Cerithidea scalariformis*, shell aperture, showing retracted animal with pallial eye exposed. I, *Terebralia sulcata*, spermatophore. J, *Terebralia sulcata*, loosely coiled spawn mass about 30 mm long. apg, anterior pedal gland; clg, ciliated groove; com, columellar muscle; cpt, cephalic tentacle; exs, exhalant siphon; eye, eye; ins, inhalant siphon; llg, left lateral groove; mae, mantle edge; mnp, mantle papillae; mo, mouth; omc, opening to mantle cavity; op, operculum; ov, ovary; ovp, ovipositor; pov, pallial oviduct; pse, pallial siphonal eye; sn, snout; sol, sole of foot; sts, style sac; vgr, ventral groove. (D, I, J, from Houbrick 1991; E, F, after Houbrick 1991; G, H, after Houbrick 1984c)

[A–C, R. Plant; E–H, A.J. Hill]

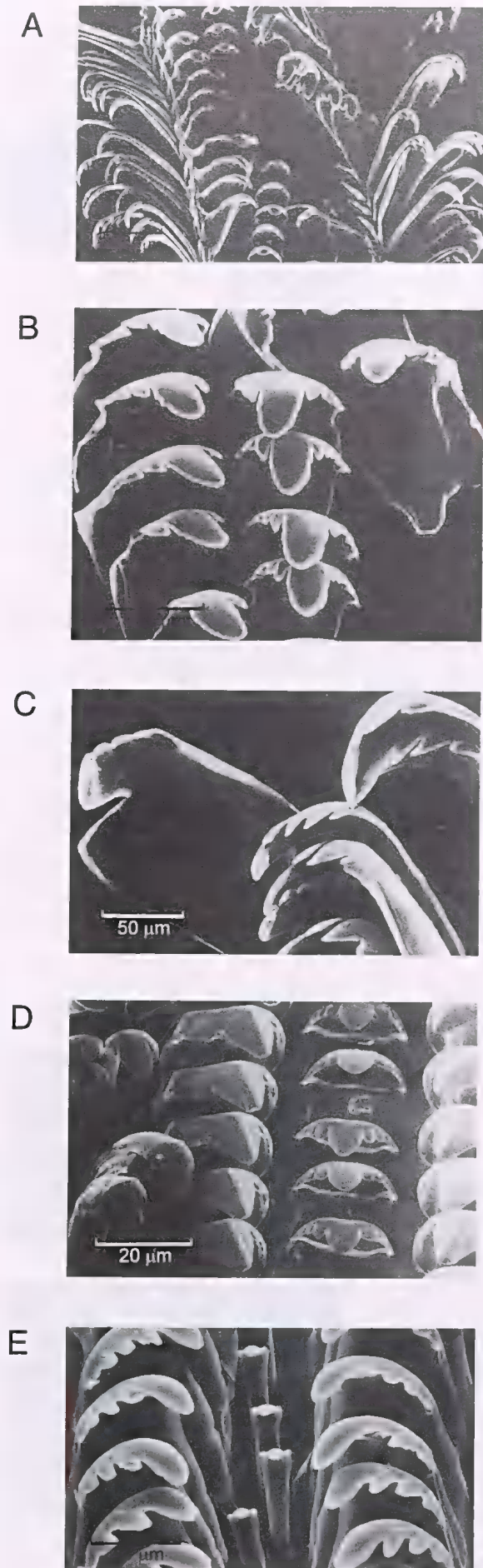


Figure 15.93 Family Potamididae. Portions of radulae. A–C, *Telescopium telescopium*: A, transverse rows of teeth; B, details of central and lateral teeth; C, details of marginal teeth. D, *Terebralia sulcata*, several half-rows of teeth. E, *Cerithidea anticipata*, details of central and lateral teeth; note the narrow central tooth. (A–D, from Houbrick 1991; E, from Houbrick 1986b)

The following summary of anatomical features derives largely from the studies of Houbrick (1984c, 1986b, 1988, 1991) and sources he cites therein. The head-foot (Fig. 15.92E–G) features a prominent, extensible, often broad snout with a median groove; short to long cephalic tentacles, each with an eye near its base; and a moderately short and broad foot with an anterior pedal gland restricted to the anterior sole margin. Details of the radulae are illustrated in Figure 15.93. Each tooth row of the radula has a rounded or tall-narrow central tooth, with a large central cusp flanked by one to five smaller cusps on each side, and always lacking denticles on the basal plate. The lateral teeth have a variable number of cusps and short to medium length lateral extensions. Marginal teeth are long, terminally curved and have well-developed cusps. The mantle edge is almost smooth and often has a light-sensitive pallial eye of varying complexity. The mantle cavity contains a thin, ridge-shaped osphradium; a ctenidium with filaments of varying length or reduced to fine ridges (ctenidium reduced, sometimes almost vestigial in amphibious species); a hypobranchial gland; a renal organ; the rectum; and gonoduct. The pair of salivary glands usually passes through the nerve ring (except in – *Terebralia semistriata*); the glands are uncoiled or slightly coiled. Oesophageal glands are absent. The stomach is well developed and has a well-developed, elongate style sac, and a long to very long crystalline style. According to Driscoll (1972), the style of *Cerithidea californica* is firm but flexible and will not dissolve in sea water, 70% isopropyl alcohol or Bouin's fixative (contrasting with the readily dissolved style of the Batillariidae). The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion and short cerebropedal connectives. Zygoneury is present. A pallial siphonal ocellus is present (Fig. 15.92H). Potamidids are dioecious and both sexes have open, structurally complex pallial gonoducts (with medial fusions in *Terebralia*). Males produce spermatophores, which in *Terebralia sulcata* (and possibly other species of *Terebralia*) are crescentic and transversely plicate (Fig. 15.92I). Euspermatozoa correspond to Healy's (1983) Group 2; paraspermatozoa are essentially of the basic cerithioid type, but with the nuclear core extending into the basal invagination of the acrosome-like structure. Spawn masses (Fig. 15.92J) consist of numerous eggs laid in jelly strings, sometimes overlain with an outer jelly layer (350 to 4800 eggs in *Cerithidea sensu lato*; up to 50 000 in *Telescopium telescopium* – Natarajan 1958; Ramamoorthi & Natarajan 1973; Houbrick 1984c). A well-developed ovipositor is present. Development is usually indirect, with a planktonic veliger larval stage, but may be direct (hatching as juveniles) in certain species of *Cerithidea* (all species of subgenus *Cerithideopsis* – Houbrick 1984c).

Potamidids are essentially mangrove gastropods. The genera *Telescopium* (with one species, *Telescopium telescopium*) and *Terebralia* (with three species, *Terebralia palustris*, *T. semistriata* and *T. sulcata*) are common, well-known inhabitants of the sand and mud surface in various parts of mangroves throughout the Indo-West Pacific (including northern Australia; Cotton 1959b). *Terebralia* species occupy different microhabitats within an individual mangrove, *T. sulcata* preferring a firm, sandy-mud substratum (Wells 1980a). In contrast, *Telescopium telescopium* and *Terebralia palustris* usually prefer very fine mud – the latter, however, favouring areas of mangrove shade (Wells 1980a; Houbrick 1991). Houbrick (1991) notes that in *Terebralia palustris*, adults and juveniles exhibited preferences for different areas of the mangrove. This species also appears to be the largest known living potamidid – the maximum recorded shell length being 190 mm (Loch 1987a). *Terebralia palustris* is also notable because its radular microstructure (especially central and laterals) becomes modified during the transition from juvenile to adult when the diet changes from fine detrital material to mangrove leaves, fruits and propagules on the mud surface (Annandale 1924; Sewell 1924; Nishihira 1983; Houbrick 1991).

Several studies have demonstrated the remarkable tolerance of potamidids to desiccation, starvation and wide fluctuations in temperature and salinity (Alexander & Rae 1974; Soemodihardjo & Kastoro 1977; Houbrick 1991; Rambabu & Rao 1992).

Five species of *Cerithidea* occur in Australia, each occupying a preferred habitat within mangrove ecosystems from southern Queensland to northern Australia. *Cerithidea cingulata* occurs on tropical mudflats both shoreward and seaward of the mangroves, but rarely lives among the trees. *Cerithidea largillierti* occurs among trees near the back of the mangrove, remaining partially buried in the sand during neap tides, and emerging only on spring tides. *Cerithidea obtusa*, *C. anticipata*, and *C. reidi* all occur on the lower portions of mangrove tree trunks or sometimes attached to the leaves; the latter two are Australian endemics, and *C. reidi* is the largest extant species in the genus (Houbrick 1986b). In tree-climbing species (*Cerithidea sensu stricto*), shell weight is reduced through loss of the apex (decollation) and production of a thin-walled shell (Houbrick 1984c; McMahon 1985). Wells (1985) examined the distribution of *Cerithidea* in Hong Kong, and showed that even within a small mangrove ecosystem the three species present occupy different microhabitats. Other ecological studies of *Cerithidea* species include those by Vohra (1970) and Rao & Sukumar (1982) on *C. cingulata* in Singapore and India, respectively.

Although the Potamididae seem to have arisen some time in the Cretaceous, it is only during the Tertiary that 'modern' genera first appear. *Terebralia* and *Telescopium*, for example, extend back to the mid Tertiary, with extant species dating from the Miocene (see Houbrick 1991). Although both genera occur widely as fossils throughout the later Tertiary of South-East Asia (with *Terebralia* also occurring in the Pliocene of New Guinea), neither has been recorded from Australian deposits (see Houbrick 1991 for references). All Recent species in these genera have an Indo-Pacific distribution (Houbrick 1991). Similarly, the genus *Cerithidea* can be confirmed as fossils only from the Miocene (subgenera *Cerithidea sensu stricto*, *Cerithiopsilla*), with records of Cretaceous species possibly applying to unrelated potamidid taxa (see Houbrick 1984c for discussion). Houbrick (1984c) noted that when compared with fossil potamidids, Recent members of the family (with some exceptions) exhibit a trend towards reduction in the expansion of the outer lip. He also considered that within the Potamididae, the potential for convergence in characters such as those associated with the shell, was probably high, and that further anatomical information was required to resolve taxonomic problems within the group.

Family Thiaridae

This large, almost cosmopolitan family (= Melaniidae) occurs in a variety of fresh- and brackish-water habitats especially throughout the tropics where certain species have proved to be prolific and rapid colonisers. Thiarids are of considerable biological and economic importance because they act as intermediate hosts for a variety of trematode parasites of fish, domesticated animals and humans (lung flukes). Houbrick (1988) emphasised several significant anatomical characteristics of the Thiarinae, including the presence of salivary glands anterior to the nerve ring, a weak hypobranchial gland, loss of the basal extension on the central tooth of the radula, usually parthenogenetic reproduction and a closed pallial oviduct. The last feature is probably derived and is unique among cerithioideans. The relationships between the various proposed subfamilies of Thiaridae are very uncertain, and it is doubtful that these groups truly constitute a monophyletic unit (Houbrick 1988). Some, like the Melanopsinae (occurring in Europe, New Caledonia and New Zealand) have long been recognised as families in their own right by a number of authors (for example, Morrison 1954; Boss 1982; Ponder & Warén 1988). In this account, we limit the concept of the family Thiaridae *sensu stricto* to the Thiarinae. The Thiaridae are the only freshwater cerithioidean family confirmed as being present in the Australian fauna.

The shell (Fig. 15.94A–C) is robust, thick to thin, turreted (often showing a stepped spire) and commonly shows some degree of decollation when mature. The aperture is round to ovoid and entire, typically without an anterior siphonal notch (notch present

in some, but never developed into a canal). Sculptural features include spiral ridges often complemented with nodules or short spines on the shoulder of the body whorl. Shell colour may range from black to brown to yellow mottled with brown spots or flammules. Environmental erosion and/or mineral deposits may greatly affect the appearance and colour of the shell. The periostracum is usually thin and is often missing from the spire due to decollation and erosion. The operculum is oval and paucispiral with an eccentric or central nucleus.

The following summary of the anatomical features of the Thiaridae is based on characters as listed by Houbrick (1988), combined with information from various sources, notably Starmühlner (1969), Berry & Kadri (1974), Muley (1977, 1978a, 1978b). The head-foot has a moderately long extensible snout, long cephalic tentacles each with an eye at the base, an anterior pedal gland not confined to the anterior edge of the foot, a subhaemocoelic brood pouch (Fig. 15.94D, F) and an ovipositor. The mantle edge is fringed by many papillae positioned on the top half of the mantle (Fig. 15.94D). Within the mantle cavity are a long, ridge-like (simple) osphradium (length slightly less than the gill length); a long ctenidium with long filaments; a weakly developed hypobranchial gland lacking distal leaflets; a renal organ; the rectum; and gonoduct (Fig. 15.94D, F). Each tooth row of the radula (Fig. 15.94G) has a quadrate central tooth with a large central cusp flanked on each side by two to four smaller cusps and a basal edge with a pair of baso-lateral projections. The rhomboidal lateral teeth have one small inner cusp, a large terminal cusp and two to three small cusps on the outer edge. The inner and outer marginal teeth both have a large outer cusp and two smaller inner cusps. The alimentary tract is illustrated in Figure 15.94E. The paired salivary glands are uncoiled or slightly coiled and lie above and anterior to the nerve ring. An oesophageal gland is present. The stomach contains a short style sac, a crystalline style and a gastric shield. Thiarids are essentially detritus feeders, but Smith (1992) notes that some species may also ingest algae. The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion, elongate extensions of the pedal ganglia and long cerebropedal connectives. Zygoneury is absent. Typically, thiarids are parthenogenetic (with occasional males), but some are gonochoristic. The female pallial gonoduct is unusual among the Cerithioidea in being closed throughout its length and associated with many transverse, glandular folds. Females develop an extensive brood pouch within the mantle cavity (Fig. 15.94D, F). The pouch, at least in *Thiara scabra*, contains a slightly alkaline, albuminous fluid (Muley 1977). Young of varying ages develop within the pouch, passing through trochophore and veliger stages (Ramamoorthi 1955; Muley 1978a), before eventually being expelled as juveniles via the birth pore on the right side of the head. Exceptionally, young are released as veligers (see Seshaiya 1940; Dudgeon 1982). Males, when present, are aphyllid and may produce dimorphic spermatozoa (in some species only abortive spermatogenic cells are produced). The euspermatozoa of *Melanoides* (*Melanoides*) *tuberculata* most closely approach those of Group 2 of Healy (1983) but have a long nucleus virtually penetrated by the axoneme, and apparently no midpiece flange structures at the neck region (Kohnert & Storch 1984a; Hodgson & Heller 1990). The paraspermatozoa of this species are multiflagellate and lack a condensed nuclear core (Hodgson & Heller 1990). It is uncertain whether thiarids, like other cerithioideans, produce spermatophores. Basic features of the embryology of *Thiara scabra* (as *Melania scabra*) have been outlined by Muley (1978a).

Few detailed taxonomic studies of the Thiaridae have been published, although some have contributed valuable data on comparative anatomy and functional morphology. Morrison (1954) assessed family, genus and subgenus-level taxa among the world's freshwater 'melanians' (= Thiaridae *sensu lato* of early authors) and concluded that the Pleuroceridae, Melanopsidae and Thiaridae *sensu stricto* probably had independent marine origins. Major systematic studies have dealt with the thiarids of Africa (Moore 1898; Binder 1959), Madagascar (Starmühlner 1969),

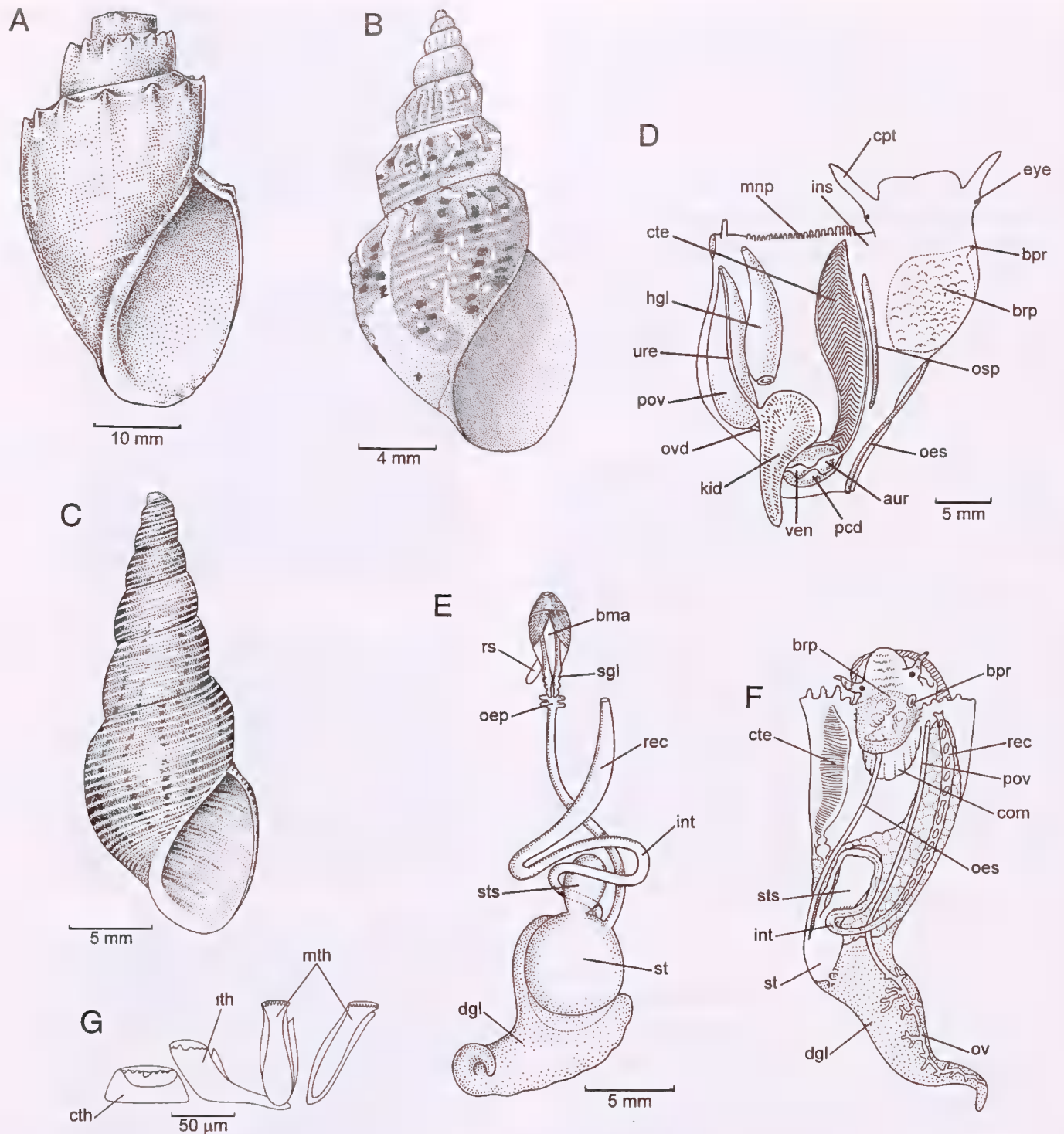


Figure 15.94 Family Thiariidae. A–C, shells, apertural view: A, *Thiara (Thiara) amarula*; B, *Thiara (Plotiopsis) balonnensis*; C, *Melanoides tuberculata*. D, *Thiara (Thiara) amarula*, diagram of dissected female showing head, brood pouch and organs of the mantle cavity. E, *Thiara (Thiara) amarula*, alimentary tract. F, *Melanoides (Melanoides) tuberculata*, dissected female showing reproductive organs and young in brood pouch. G, *Thiara (Thiara) amarula*, half of radular tooth row. **aur**, auricle; **bma**, buccal mass; **bpr**, brood pore; **brp**, brood pouch; **com**, columellar muscle; **cpt**, cephalic tentacle; **cte**, ctenidium; **cth**, central tooth; **dgl**, digestive gland; **eye**, eye; **hgl**, hypobranchial gland; **ins**, inhalant siphon; **int**, intestine; **kid**, kidney; **lth**, lateral tooth; **mnp**, mantle papillae; **mth**, marginal teeth; **oep**, oesophageal pouch; **oes**, oesophagus; **osp**, osphradium; **ov**, ovary; **ovd**, oviduct; **pcd**, pericardium; **pov**, pallial oviduct; **rec**, rectum; **rs**, radular sac; **sgl**, salivary glands; **st**, stomach; **sts**, style sac; **ure**, ureter; **ven**, ventricle. (D, E, G, after Starmühlner 1969; F, after Berry & Kadri 1974) [A, C–G, R. Plant; B, C. Eadie]

Indonesia (Bentham Jutting 1956, 1963), the Pacific Islands including New Guinea and New Caledonia (Starmühlner 1970, 1976, 1992, 1993) and the Americas (Pilsbry & Hinkley 1909; Morrison 1954). In addition, Kollmann (1984) revised fossil species from the Upper Cretaceous of the European Alps. Starmühlner (1969, 1970, 1976, 1992, 1993) has examined aspects of thiarid taxonomy, biology and distribution in the islands of the Pacific and Indian Oceans, and gave histological details for several species. The synonymies given by Starmühlner and Bentham Jutting in their monographs are particularly useful (numerous names have been proposed in the literature).

A number of studies have been made of the biology of thiarids to assist in control of human parasites or to provide basic data on the group. Species studied include *Paludomus tanschaurica* (Seshaiya 1934) and *Thiara scabra* (as *Melania scabra* – Muley 1977, 1978a, 1978b) in India; *Brotia hainanensis* in Hong Kong (Dudgeon 1982); and *Melanoides (Melanoides) tuberculata* in Israel (Livshits & Fishelson 1983), Guadeloupe (Pointier, Théron & Borel 1989; Pointier, Delay, Toffart, Lefèvre, & Romero-Alvarez 1992) and Hong Kong (Dudgeon 1986). Other studies of *M. (M.) tuberculata* include those of R.T. Abbott (1952), Chaniotis, Butler, Ferguson & Jobin (1980a, 1980b, 1980c) and Pointier (1989).

One of the most interesting features of thiarid biology is the widespread occurrence of parthenogenesis as a reproductive strategy. Males are unknown in many species, but regularly occur in low numbers in some species or at least in certain populations of these species. For example, populations of *Melanoides (Melanoides) tuberculata* in Israel usually have males (Livshits & Fishelson 1983; Livshits, Fishelson & Wise 1984), whereas in most other areas of the world males of this species are either extremely rare or unknown. Major variations in chromosome number may occur between populations as a result of polyploidy (normal chromosome number 32, 90–92 in polyploid populations – Jacob 1957, 1958). By eliminating the need for mating, parthenogenesis has the potential to facilitate greatly snail dispersal into new areas. Stoddart (1983, 1985) examined the genetic consequences of parthenogenesis in an Australian species, *Thiara (Plotiopsis) balonnensis*. Of the 13 populations investigated by Stoddart (1983), all but one consisted of a single clone. Geographically close populations were the most similar genetically. Stoddart (1983, 1985) postulated that this pattern was a result of mutation and loss of alleles after the populations became geographically separated.

Aside from the genetic work of Stoddart (1983, 1985) and brief notes in faunal lists (Tate & Brazier 1882; Iredale 1943) or books or chapters (McMichael & Iredale 1959; Smith & Kershaw 1979), the biology of Australian thiarids remains essentially unstudied, which is surprising given the well-demonstrated medical and ecological significance of thiarids in other parts of the world. Smith (1992) recognised ten species: one each from the genera *Brotia*, *Ripalania*, *Sermylasma*, four in the genus *Melanoides* (one from subgenus *Melanoides*, three from subgenus *Stenomelania*) and three in the genus *Thiara* (one in subgenus *Thiara*, two in subgenus *Plotiopsis*). All except two of these species are native. A further six species, of various generic assignments, were listed by Smith as *incertae sedis*, indicating an obvious need for detailed comparative studies of local material. Stoddart (1983) has argued that *Plotiopsis* and *Melanoides* are probably both synonyms of *Thiara*, whereas McMichael & Iredale (1959) has suggested that Iredale's genera *Sermylasma*, *Ripalania* and *Pseudopotamis* need re-evaluation. Smith (1992), however, has retained all of these taxa as valid, but made *Plotiopsis* a subgenus of *Thiara*. Anatomical and molecular studies need to be carried out on Australian native thiarids, to test the validity of the currently recognised genera.

Melanoides (Stenomelania) denisoniensis occurs in coastal rivers from northern New South Wales to Cape York in far northern Queensland, and along with the possibly introduced *Melanoides (Melanoides) tuberculata*, is one of the more common northern species. In fact the majority of Australian thiarids are limited essentially to the northern half of the continent (Smith 1992). The most widespread of the temperate Australian species is *Thiara (Plotiopsis) balonnensis* which occurs in rivers and ponds (and dams) from South Australia east and north to southern Queensland (Smith 1992).

The origin of Australian populations of the ubiquitous *Melanoides (Melanoides) tuberculata* is uncertain. According to Smith (1992), the species has been introduced from an 'unknown country'. Currently, it occurs in freshwater and estuarine habitats primarily in northern parts of Australia from the Gulf of Carpentaria west to Western Australia (Smith 1992). Although a known intermediate host of certain freshwater digenean worms in Asia (see Cribb, Bray & Barker 1992) it is unknown whether this species is involved in the life cycle of any Australian digeneans. Outside Australia, *M. (M.) tuberculata* is now distributed throughout the tropical regions of the world, including most island groups both in the Indo-Pacific and Caribbean (Starmühlner 1969, 1993). The spread of this species is due primarily to its ability to colonise rapidly and to dominate freshwater habitats – the result of parthenogenesis in combination with a short sexual maturation time (Berry & Kadri 1974; Dudgeon 1989) and tolerance of salinity fluctuations and desiccation. This has led to *M. (M.) tuberculata* being deliberately introduced as a competitor

species to reduce populations of various species of the freshwater pulmonate genus *Biomphalaria* (intermediate hosts for human schistosome parasites), with some degree of success (Pointier, Guyard & Mosser 1989; Pointier, Toffart & Lefèvre 1991; Pointier, Théron & Borel 1993).

Groups that were once included (for example, Thiele 1929–1935) within the Thiaridae ('Melaniidae') *sensu lato* are the Melanopsidae and Pachychilidae ('Pleuroceridae'). Like Morrison (1954), Houbbrick (1988) believed that the Thiaridae *sensu lato* are probably polyphyletic, and in his phylogenetic analysis of cerithioidean relationships only considered features of the subfamily Thiarinae for character scoring of the Thiaridae. Houbbrick's study showed the Thiaridae to belong to a clade with the Planaxidae and Diastomatidae.

There appear to be no published records of fossil thiarids from the Australian region.

Family Diastomatidae

This small family, once widespread in shallow Tertiary seas, is today represented by a single extant species *Diastoma melanioides*, living in sandy seagrass habitats along the south-eastern coast of Australia. Diastomatids are characterised by turreted shells that have fine cancellate sculpture and lack an anterior siphonal notch. According to Houbbrick (1981c), several anatomical features of *Diastoma melanioides* are unusual for cerithioideans and presumably can be regarded as diagnostic of the Diastomatidae as a whole. These are a highly extensible snout and a large cephalic cavity; unusually long and simple salivary glands; muscle strands connecting the anterior and mid-oesophagus to the cephalic cavity; a simple pallial gonoduct; a large, complex, internal ovipositor; long labial and buccal nerves, with innervation of the ovipositor by the mesopodial ganglion; and the proximal ends of the osphradium, ctenidium and hypobranchial gland beginning near the anterior end of the mantle cavity instead of the posterior end as occurs in most cerithioideans.

Diastomatid shells are turreted and elongate with cancellate sculpture; varices may be present. They have an oval aperture, a wide almost obsolete anterior siphonal canal, no anal canal posteriorly, and a deeply impressed suture and ramp. *Diastoma melanioides* (Fig. 15.95A) has a shell length of 30–50 mm, and the periostracum is covered with short bristles that are especially visible on fresh, live-collected specimens. The protoconch of *D. melanioides* consists of two smooth whorls and is delineated from the teleoconch and its cancellate sculpture by a straight lip (Fig. 15.95B). The operculum is oval, dark brown, corneous and paucispiral (Fig. 15.95C; Houbbrick 1981c).

The anatomical features listed below are based on studies of preserved animals of *Diastoma melanioides* by Houbbrick (1981c, 1984a, 1988). The head-foot (Fig. 15.95D) has a long, extensible snout, long cephalic tentacles each with an eye at the base, an anterior pedal gland and an ovipositor. The mantle edge is fringed by many papillae positioned on the top half of the mantle. The mantle cavity (Fig. 15.95D) contains a long, bipectinate osphradium, a long ctenidium with long filaments, a well-developed hypobranchial gland, a renal organ, the rectum and gonoduct. Thin jaws are present. Each tooth row of the radula (Fig. 15.95E) has a quadrate central tooth with a large central cusp flanked on each side by two to four smaller cusps, and a basal edge with a pair of baso-lateral projections. The rhomboidal lateral teeth have a cutting edge with an inner denticle, a large terminal cusp and two or three smaller cusps. The inner and outer marginal teeth both have a large outer cusp and two smaller inner cusps. The pair of salivary glands passes through the nerve ring. An oesophageal gland is absent. The stomach contains a short style sac and crystalline style, and a gastric shield. The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion, elongate extensions of the pedal ganglia and short cerebropedal

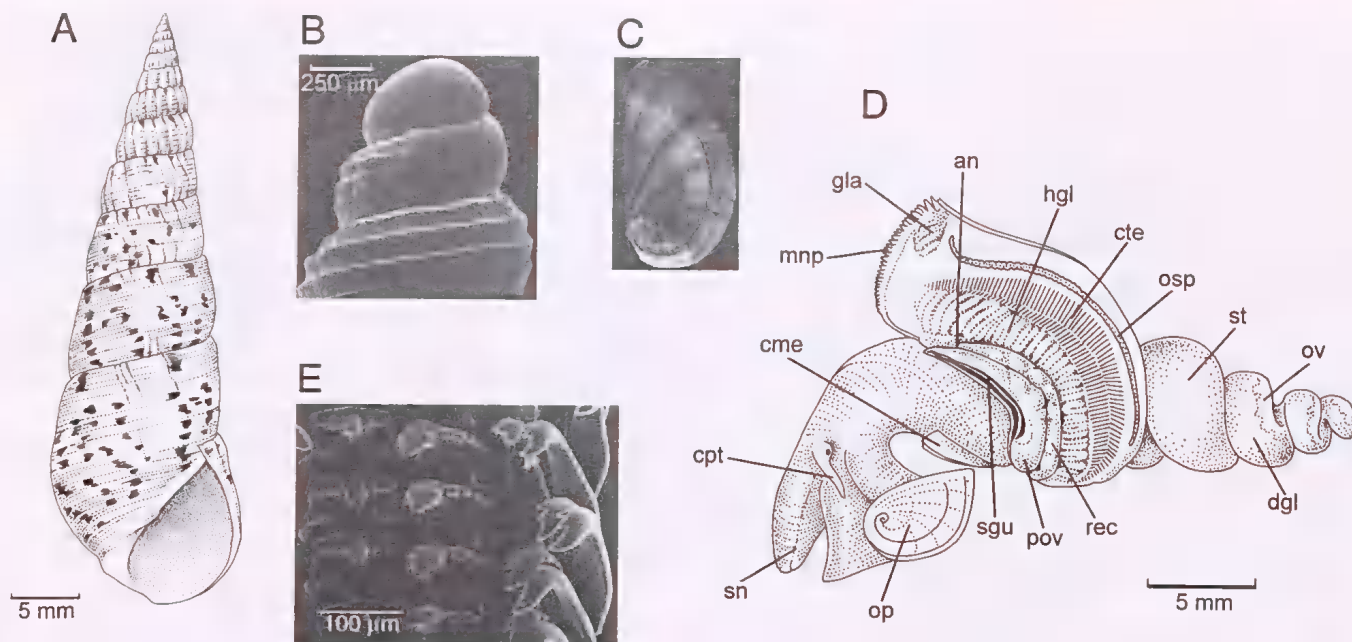


Figure 15.95 Family Diastomatidae. *Diastoma melanioides*: A, shell, apertural view; B, protoconch showing change from embryonic to juvenile shell sculpture; C, operculum, outer surface; D, female removed from shell, and mantle cavity opened along and viewed from left side; E, four half transverse rows of radular teeth. an, anus; cme, cut mantle edge; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; gla, glandular area in mantle cavity; hgl, hypobranchial gland; mnp, mantle papillae; op, operculum; osp, osphradium; ov, ovary; pov, pallial oviduct; rec, rectum; sgu, sperm gutter; sn, snout; st, stomach. (B, C, E, from Houbrick 1981c; D, after Houbrick 1981c) [A, D, R. Plant]

connectives. It is uncertain whether zygoneury is present or absent. The pallial gonoduct of the female is more developed than that of the male and is associated with many transverse, glandular folds. Sperm ultrastructure has yet to be investigated. Sperm appear to be packaged in spermatophores.

Little is known of the ecology of *D. melanioides*. It lives in shallow subtidal sand at depths of 1–5 m in areas where there are seagrass beds and macroalgae (Houbrick 1981c, 1984a) from Streaky Bay, South Australia, to Cheyne Beach, 60 km east of Albany, Western Australia. Houbrick (1981c) suggested that it feeds on microalgae and detritus in the sand, using the small radula. Animals have been observed in pairs in June (early winter) and have active ovaries in July indicating that this may be a winter-breeding species (Houbrick 1981c). On the basis of its bulbous protoconch and restricted distribution, Houbrick considered it likely that *D. melanioides* has direct development.

The family Diastomatidae, was established by Cossmann (1894) (originally 'Diastomidae', emended by Ludbrook 1971) to include a number of fossil cerithioidean genera with small shells. Cossmann and most later authors were apparently unaware of the single extant species of *Diastoma*, *D. melanioides*, living in the shallow littoral waters off the south-western Australian coast, because this species was originally placed in the turritellid genus *Mesalia*. Confusion over the limits of the family resulted in a number of additional genera being included erroneously by subsequent authors (for discussion see Houbrick 1981c). Tate (1893a), was the first to recognise *Mesalia melanioides* as a species in *Diastoma*. Houbrick (1981c, 1984a) has published the only studies of living *Diastoma*. His work resulted in the redefinition of the Diastomatidae and the exclusion of all extant taxa from the family except *Diastoma melanioides*. According to Houbrick (1981c), the family also contains 13 extinct species, all similar conchologically to *D. melanioides*, though generally with more rugose sculpture. Houbrick also rejected Cotton's (1932) decision to place *Diastoma melanioides* in its own genus *Neodiastoma*. Ponder & de Keyser (1992) considered that the Australian fossil genus *Mereldia* shows strong similarity to shells of *Diastoma*, and should be placed within the Diastomatidae. On the basis of shell characters many fossil species can be included with reasonable certainty within the family. Such fossils indicate that diastomatids were particularly prolific in the Tethys Sea

(Houbrick 1981c). Fossil *Diastoma* species are known from the Eocene and Oligocene of the Paris Basin (Houbrick 1981c). Ludbrook (1971, 1978) recorded two extinct Australian species, the earliest of which is from the Lower Miocene. She also noted that *Diastoma melanioides*, is abundant in Pleistocene deposits of the Roe Plain (Eucla Basin, Western Australia). Houbrick (1981c) suggested that the Diastomatidae may be related to the Cerithiidae, Potamididae and possibly the freshwater Melanopsidae. Recent cladistic studies suggest links between the Diastomatidae and the Planaxidae and Thiaridae (Houbrick 1988; Ponder 1991b).

Family Modulidae

The Modulidae are a warm-water group of cerithioideans occurring in the Atlantic and Indo-Pacific regions. The family is represented by the genus *Modulus* which contains about six Recent species. Although most modulids live on intertidal seagrass beds, some species occur on the undersides of coral boulders. Characteristic features such as the trochoid-turbiniform shell (with columellar tooth), structure of the cephalic tentacles and shape and positioning of certain internal organs (salivary glands) clearly distinguish this family from other cerithioideans.

Modulids have a low-spired, robust, turbiniform to trochoidal shell, 10–25 mm in length with an umbilicus and a columellar tooth (Fig. 15.96A). Five to six whorls are present and the shell may be coloured in some species. Sculpture is spiral and sometimes coarsely nodular. The protoconch of *M. modulus* is composed of two whorls ornamented with five or six spiral ridges. The periostracum is thin and tan in colour. The operculum is corneous, round, multispiral and has a central nucleus.

Risbec (1927) presented anatomical information on *Modulus tectum* (as *M. candidus*), however, several of his observations were found to be incorrect by Houbrick (1980a). For this reason the following summary of anatomical features of the Modulidae is based primarily on details presented by Houbrick (1980a, 1988 – *M. modulus*, *M. tectum*) with supplementary information from other recent sources. The head-foot (Fig. 15.96C) has a moderately long, broad extensible snout (indented terminally), long cephalic tentacles each with a thin apical region (one third of tentacle) and a thick basal region (two thirds of tentacle). The dorsal, distal third of

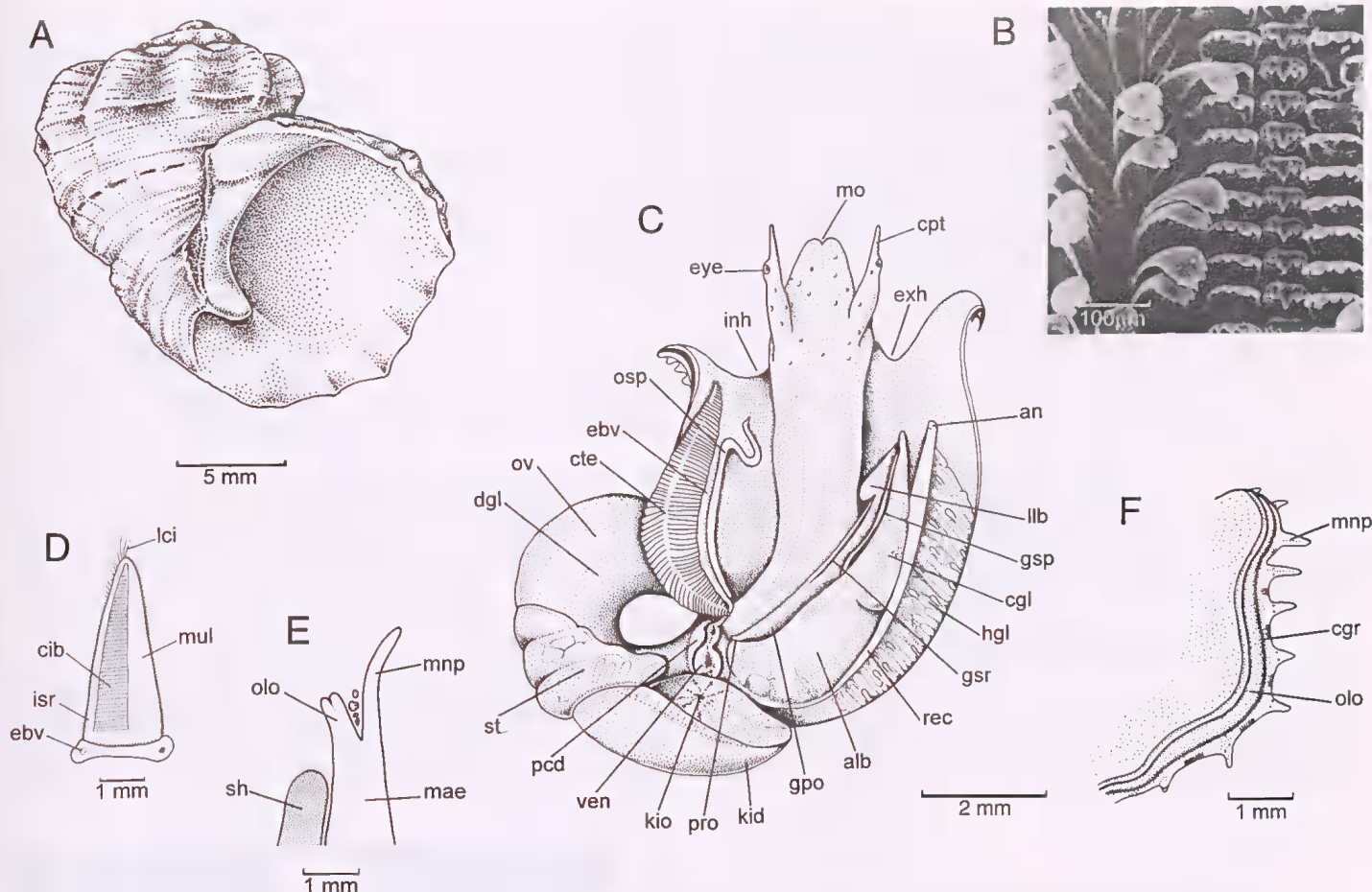


Figure 15.96 Family Modulidae. A, *Modulus tectum*, shell, apertural view. B–F, *Modulus modulus* from Florida, radula and anatomical features: B, portion of radula; C, female with the mantle cavity opened; D, individual ctenidial filament; E, mantle edge in cross-section; F, mantle edge, dorsal view, showing mantle papillae and ciliated groove. alb, albumen gland; an, anus; cgl, capsule gland; cgr, ciliated groove; cib, ciliated band; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; ebv, efferent branchial vessel; exh, exhalant aperture; eye, eye; gpo, groove of pallial oviduct; gsp, groove leading to spermatophore receptacle; gsr, groove leading to seminal receptacle; hgl, hypobranchial gland; inh, inhalant aperture; isr, internal strengthening rod of ctenidial filament; kid, kidney; kio, kidney opening; lci, long cilia; llb, baffle of lateral lamina; mae, mantle edge; mnp, mantle papillae; mo, mouth; mul, muscle band; olo, outer lobe of mantle edge; osp, osphradium; ov, ovary; pcd, pericardium; pro, proximal portion of pallial oviduct; rec, rectum; sh, shell; st, stomach; ven, ventricle. (B, from Houbriek 1980a; C–F, after Houbriek 1980a)

[A, R. Plant; C–F, A.J. Hill]

each tentacle has a ciliated band. A small eye is positioned at the commencement of the ciliated band of each tentacle. The foot is broad, but short, and has an anterior pedal gland. The mantle edge is fringed by many papillae positioned on the top half of the mantle (Fig. 15.96E, F). Within the mantle cavity are contained a long, ridge-shaped osphradium (two-thirds of ctenidial length), a large ctenidium with elongate filaments (Fig. 15.96D), a well-developed and elongate hypobranchial gland, a renal organ, the rectum and gonoduct (Fig. 15.96C). The columellar muscle is well developed and enables strong twisting motions of the animal. Animals are microalgal grazers. A pair of ovate jaws are present. Each tooth row of the radula (Fig. 15.96B) has a round-quadrate central tooth with a large central cusp flanked on each side by two or three small cusps, and a smooth basal plate. The trapezoidal lateral teeth have one small inner cusp, a larger main cusp and three or four small, outer cusps. The inner and outer marginal teeth are terminally spatulate with five or six blunt, small cusps. The left salivary gland is four-lobed, twice the size of the right (three-lobed) and passes through the nerve ring, whereas the right lies in front of the ring. A well-developed oesophageal gland (the mid-oesophageal region) is present. The stomach complex features a short wide style sac, a short, dumbbell-shaped crystalline style and a strongly developed, thick, cuticular gastric shield. The nervous system features long connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion and short cerebropedal connectives. Zygoneury is present. The female system features a spermatophoral bursa, seminal receptacle and a glandular epithelium which probably functions as an albumen gland. Males produce small (length 1–3 mm), crescentic, keeled spermatophores. Euspermatozoa correspond to Group 2 of Healy (1983) (*M. tectum* – Healy unpublished data); the paraspermatozoa have a long head

and multiple flagella (*M. modulus* – Houbriek 1980a; internal structure unknown). Development may be either direct, as in *M. modulus* (Florida population, Houbriek 1980a), or indirect as in *M. carchedonius* (Bandel 1976a). Development to the veliger stage takes five to six days.

Houbriek (1980a) traced the complete life cycle of *M. modulus*. Gametes ripen during the winter and spawning begins in spring, continuing for several months. The population thus contains, at any one time, several classes of young varying in age from one to several months. Spermatophores from males are manipulated in the female mantle cavity by ciliary currents. Females deposit eggs in cylindrical gelatinous tubes that are attached to seagrass blades. Each egg mass contains 70 to 169 eggs, and each female deposits more than one egg mass (Houbriek 1980a; compare with 7000 eggs in *M. carchedonius* – Bandel 1976a). Crawling juveniles hatch after 18 days. Maturity is reached after one year, and the animals die after spawning.

The only substantial study of living modulids is that by Houbriek (1980a) on *Modulus modulus* from Florida. In contrast to *M. tectum*, a widespread Indo-Pacific species (occurring in tropical Australia) that lives under coral rock, *M. modulus* lives on seagrass blades in shallow water. It browses actively on diatoms on the seagrass blades; microalgae and detritus are also included in the gut contents. Houbriek (1980a) noted that *M. modulus* produces large quantities of mucus-like globular particles when disturbed, but he could not determine the function of this activity. In contrast, he found that *M. tectum* does not produce these particles if disturbed, but like *M. modulus* (and possibly all other modulids), does exhibit strong twisting movements.

15. PROSOBRANCHS

The precise relationship of modulids to other cerithioideans is still uncertain. Cladistic studies have suggested that the family may be linked to the Potamididae and Batillariidae (Houbrick 1988) or lie somewhere between the Turrillidae and Batillariidae (Ponder 1991b). Sperm data for modulids are very limited (scanning electron micrographs of Houbrick 1988; some transmission electron micrographs of Healy 1984). The structure of the eusperm midpiece appears to place the Modulidae with the Potamididae and Scaliolidae in Healy's Group 2, but further detailed study is needed.

Although fossil modulids are known back to the Cretaceous, there appear to be no records of fossil of this family from Australia.

Family Scaliolidae

Scaliolids are small-sized, shallow water cerithioideans found throughout the subtropical and tropical regions of the Indo-West Pacific (Ponder 1994a). This family (= Finellidae) was poorly defined until Ponder (1994a) presented a detailed diagnosis based on the two genera that he recognised as valid: *Scaliola* and *Finella*. Ponder's account of anatomy and shell morphology (including protoconch ultrastructure) combined with the results of sperm ultrastructural studies (Healy 1982c, unpublished data) have unequivocally established the cerithioidean nature of *Finella* and *Scaliola*. Eusperm features suggest that the Scaliolidae are allied to groups such as the Potamididae and Modulidae (Healy 1982c, 1983).

The shells (Fig. 15.97A, B) are 2–4 mm in length, turreted and elongate, lack varices, and are ornamented either with spiral and/or axial sculpture (cancellate in *Finella*) or unsculptured and covered with cemented sand grains, as in *Scaliola* species (Fig. 15.97G, H). The aperture is ovate and lacks an anterior canal. The protoconch is of two to two and a half whorls in *Finella* and up to four whorls in *Scaliola*, terminating in a varix with a deep sinusigeral notch (Fig. 15.97C). Protoconch sculpture in *Finella* is completely lacking in the first half whorl (protoconch I), but subsequently fine growth lines appear together with a median spiral cord (protoconch II). The operculum is rounded to ovate with a nucleus placed centrally or subcentrally (Fig. 15.97D). According to Ponder (1994a), attachment of the sand grains to the shell in *Scaliola* (a unique phenomenon in the Cerithioidea) probably occurs through foot or snout manipulation of grains against the mantle edge and cementation through the use of periostracal fluid.

The following anatomical information on the Scaliolidae derives primarily from Ponder's (1994a) study of various species of *Finella* and *Scaliola* (from Hong Kong and Queensland). The head-foot features a large, highly extensible snout and a pair of cephalic tentacles (long in *Finella*, short in *Scaliola* – Fig. 15.97A, G, H). The foot is tapered posteriorly and has an anterior pedal gland, but no posterior pedal gland. Movement proceeds by a series of forward jerks sometimes involving alternate anchoring from the anterior or posterior extremities of the foot. Three mantle tentacles, differing in length, are present in *Finella* (Fig. 15.97A), but absent in *Scaliola*. Within the mantle cavity are found the ttenidium, osphradium, hypobranchial gland, renal organ, rectum

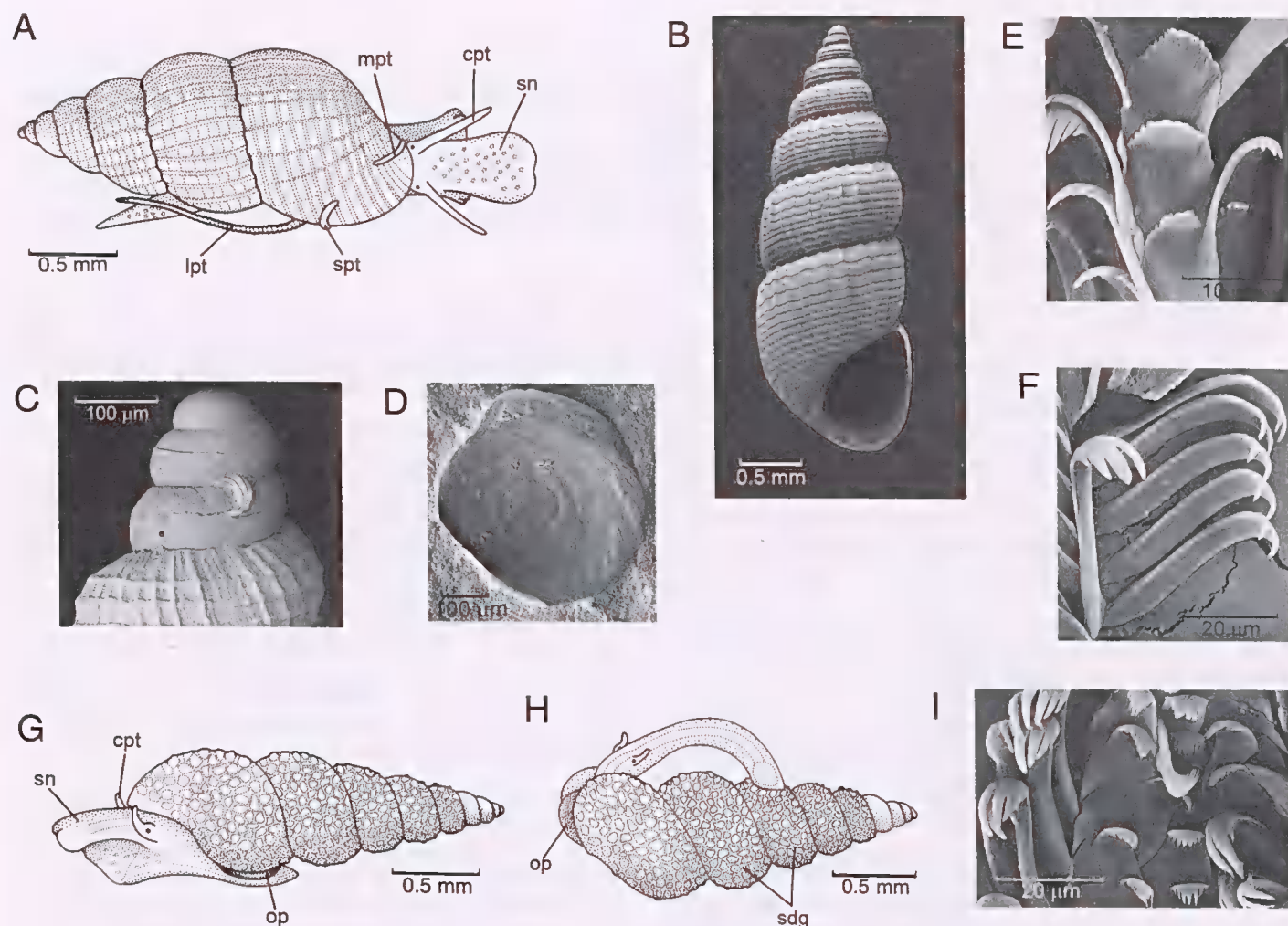


Figure 15.97 Family Scaliolidae. A–F, *Finella pupoides* (Hong Kong): A, crawling animal, dorsal view, note cancellate shell sculpture and pallial tentacles; B, shell, apertural view; C, protoconch and apical whorls of teleoconch; D, operculum; E, portion of radula showing the central and lateral teeth; F, marginal teeth of radula. G–I, *Scaliola* sp. (Hong Kong): G, animal shown crawling with snout in resting position; H, animal with snout extended, feeding on shell surface; note sand grains cemented to shell; I, portion of radula showing central, lateral and marginal teeth. cpt, cephalic tentacle; lpt, long pallial tentacle; mpt, medium pallial tentacle; op, operculum; sdg, sand grains; sn, snout; spt, short pallial tentacle. (A, G, H, after Ponder 1994a; E, F, I, from Ponder 1994a; B, C, D, courtesy of W.F. Ponder)

[A, G, H, C. Eadie]

and gonoduct. Details of radulae are illustrated in Figure 15.97E, F, I. Each tooth row of the radula has a tall quadrate central tooth with a variable number of small cusps on the convex dorsal edge and no denticles on the basal plate. The lateral teeth have a central large cusp flanked on each side by two smaller cusps, and the long, robust, terminally hooked marginal teeth have a few strong distal cusps. Detritus appears to be the principal diet of scaliolids. *Scaliola* sp. is known to feed from its shell surface (Fig. 15.97H; Ponder 1994a). Buccal pouches are present in *Finella*, but absent in *Scaliola*. Tubular salivary glands are present and pass through the nerve ring. The oesophagus, which may or may not be associated with an oesophageal gland, leads to the stomach which has a short style sac, a crystalline style and a gastric shield. The nervous system features short connectives between the cerebral ganglia, a suboesophageal ganglion close to the pleural ganglion, elongate extensions of the pedal ganglia and short cerebropedal connectives. Zygoneury is present.

Scaliolids are dioecious with a glandular oviduct in females open most of its length in the mantle cavity (closed posteriorly). Bursae are in medial or lateral lamellae and are distinct from the seminal receptacle. Spermatophores have been observed by Ponder (1994a) in *Finella* and presumably are also present in *Scaliola*. Sperm ultrastructure has been investigated in species of *Finella* and *Scaliola* (Healy 1982c, unpublished data). Euspermatozoan morphology corresponds with type 2 of Healy (1983) with pronounced differences in acrosomal morphology between *Finella fabrica* (as '*Obtortio* cf. *fulva*') and *Scaliola* sp. Euspermatozoa of *Finella fabrica* are accompanied by eusperm-like sperm (spermatozoa with a nucleus only half that of the euspermatozoan). It is not yet known whether eusperm-like sperm are present in other species of *Finella*. Paraspermatozoa of *F. fabrica* and *Scaliola* sp., like those of other cerithioideans, are multiflagellate with a distinct anterior 'head' region composed of a variable number of axonemes surrounded by dense vesicles. No condensed nuclear remnant is present in scaliolid paraspermatozoa. Nothing is known of the morphology of the spawn mass of scaliolids or details of larval development. Protoconch morphology, however, suggests the occurrence of both planktotrophic and direct development.

Despite the fact that scaliolids may be very common intertidal and littoral inhabitants of sandy-mud substrata, it is as yet impossible to estimate the number of species contained within the family. Ponder (1994a) stated that there are several species of *Scaliola*, but also noted that resolution of the taxonomy is impeded partly because of difficulties of clarifying the identity of species described by A. Adams. Species of *Finella* have usually been placed in the genus *Obtortio* by Australian authors (for example, Ludbrook 1941; Laseron 1950, 1956a; Iredale & McMichael 1962). Although Thiele (1929–1935) regarded *Obtortio* as a subgenus of *Finella*, Ponder & Warén (1988) and Ponder (1994a) recognised only *Finella* (*Obtortio* thereby relegated to the synonymy of *Finella*). There are several Indo-Pacific species of *Finella* (W.F. Ponder personal communication).

Lack of anatomical information combined with excessive emphasis on shell features has led several authors to place members of the Scaliolidae into groups as diverse as the Janthinoidea (Epitoniidae) and Rissooidea (Rissoiidae, Rissoinidae) (see Ponder 1994a for discussion of previous placements and references). Laseron (1956a) placed the genus *Obtortio* (= *Finella*) within the rissooidean family Rissoinidae, but was apparently unaware of Thiele's (1929–1935) inclusion of the genus in a distinct cerithioidean family, the Finellidae, or of Thiele's description of radular, opercular and anatomical features. Previous associations of the genus *Finella* ('*Obtortio*') with the cerithiid subfamily Bittiinae are certainly understandable given the resemblances in shell shape, size range and sculpture. However, there are many anatomical differences between the Scaliolidae and Bittiinae (see anatomical summary of Cerithiidae). The status and composition of the Scaliolidae have recently been clarified by Ponder (1994a) following a detailed anatomical study of representatives of the genera *Finella* and *Scaliola*. Although some authors have allocated *Scaliola* and *Finella* to separate

families (for example, Iredale & McMichael 1962), Ponder (1994a) concluded that anatomical differences between the two genera are not significant enough to support such action. Like Thiele (1929–1935), he placed both in a single family (now = Scaliolidae, but formerly the Finellidae or Obtortionidae).

Ludbrook (1941) described a species of *Obtortio* from the Pliocene of South Australia, but this does not belong to the Scaliolidae (W.F. Ponder personal communication). According to Bandel & El-Nakhal (1993), fossils referable to the genus *Scaliola* extend back to the Cretaceous. The actual relationships of the Scaliolidae (as presently constituted) have not been fully resolved. Bandel & El-Nakhal (1993) believed that *Scaliola* may be close to *Bittium* (Cerithiidae) or perhaps *Diastoma* (Diastomatidae). Euspermatozoan ultrastructure of scaliolids (species of *Scaliola* and *Finella*) suggests close links with the Potamididae and possibly the Modulidae, but not with *Bittium* (Cerithiidae) (Healy 1982c, unpublished data). Ponder (1994a) pointed out that there are several differences between the anatomy of scaliolids and potamidids and modulids. A possible relationship between the Scaliolidae and Diastomatidae could perhaps be tested by examining the ultrastructure of *Diastoma* spermatozoa.

Superfamily CAMPANILOIDEA

The Campaniloidea reached their peak of diversity in the early Tertiary with a radiation in the Tethys Sea (Houbrick 1981a, 1984d). The group once contained a number of genera and species and is perhaps best known from the Eocene of the Paris Basin, France. Some of the fossil species reached over a metre in length and are among the largest gastropods ever to have existed (Houbrick 1981a; Jung 1987).

The superfamily presently comprises the Campanilidae and the Plesiotrochidae which was recently transferred from the Cerithioidea on the basis of distinctive eusperm and parasperm synapomorphies between *Plesiotrochus* and *Campanile* (Healy 1993b). The results presented by Houbrick (1981a) and the increasing importance placed by molluscan systematists on characteristics such as the ultrastructure of spermatozoa and the osphradium have recently led several authors to reconsider the position of the Campanilidae. Houbrick (1988) investigated the phylogeny of the Cerithioidea, including the Campanilidae in his analysis. He listed a number of anatomical autapomorphies of the only extant campanilid, *Campanile symbolicum*: calcareous periostracum; short, oval bipectinate osphradium; anterior leaflets on the hypobranchial gland; buccal pouches; transverse septum dividing the cephalic haemocoel from the mid-oesophagus; a pit with spirally arranged leaflets within the stomach; a seminal receptacle in the pericardium; a spawn mass with chalazae-like structures connecting individual eggs; the lack of hyaline capsules around the eggs; and the distinctive sperm characteristics. Houbrick (1988) and Healy (1986b, 1988a) suggested that the Campanilidae diverged early on from the remainder of the cerithioideans. Ponder & Warén (1988) also included the Campanilidae in the Cerithioidea, but pointed out that because of its unusual characteristics a different placement might be warranted for the family. Haszprunar (1988a) concluded that *Campanile* represents a step towards euthyneurous organisation, and proposed a new suborder, the Campanilomorpha (containing superfamily Campaniloidea, family Campanilidae) which he placed between the Caenogastropoda and Heterobranchia. After studying osphradial ultrastructure in *C. symbolicum* and taking sperm ultrastructural features into account (Healy 1986b, 1988a), Haszprunar (1992b) concluded that this species is probably more closely allied to (and possibly can be included in) the Caenogastropoda than to the Allogastropoda–Euthyneura (heterobranch) assemblage. Houbrick (1989) re-investigated *C. symbolicum* and provided additional anatomical information. Houbrick (1989) concluded that *Campanile* should be placed in a separate superfamily (independently introduced by Haszprunar 1988a), Campaniloidea, which he considered to be an early offshoot from the lineage from which the Cerithioidea and other

15. PROSOBRANCHS

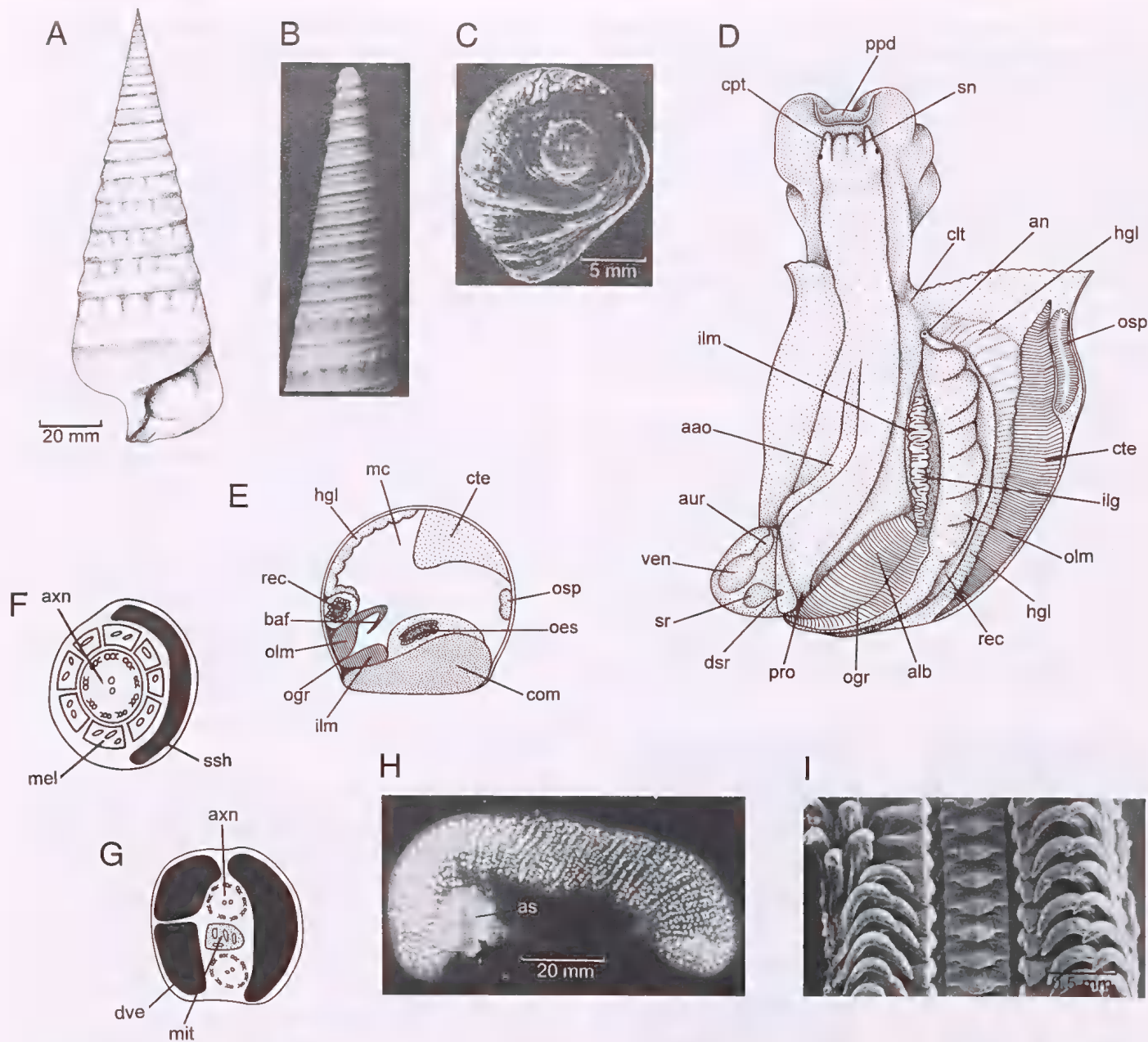


Figure 15.98 Family Campanilidae. Features of *Campanile symbolicum*: A, shell, apertural view; B, spiral nodulose sculpture on early whorls of shell; C, operculum with subcentral nucleus; D, female with mantle cavity opened showing the mantle organs; E, cross section of female through mid mantle cavity showing spatial relationship of major pallial organs; F, cross section of euspermatozoon through midpiece region; G, cross section of paraspermatozoon through 'head' region; H, spawn mass showing attachment surface – note jelly and egg strands composing spawn mass; I, several transverse rows of the radula. aao, anterior aorta; alb, albumen gland; an, anus; as, attachment surface; aur, auricle; axn, axoneme; baf, baffle; clt, ciliated tract; com, columellar muscle; cpt, cephalic tentacle; cte, ctenidium; dsr, duct of seminal receptacle; dve, dense vesicle; hgl, hypobranchial gland; ilg, glandular part of inner lamina; ilm, inner lamina; mc, mantle cavity; mel, mitochondrial element; mit, mitochondrion; oes, oesophagus; ogr, oviducal groove; olm, outer lamina; osp, osphradium; ppd, propodium; pro, proximal part of pallial oviduct; rec, rectum; sn, snout; sr, seminal receptacle; ssh, segmented sheath; ven, ventricle. (B, C, H, I, from Houbrick 1981a; D, E, after Houbrick 1981a; F, G, after Healy 1993b) [A, G, Parker; D–G, C. Eadie]

caenogastropods arose. *Campanile* (1 extant species) and *Plesiotrochus* (a few extant species) both exhibit several autapomorphies. *Plesiotrochus* shares relatively more plesiomorphies with the Cerithioidea than does *Campanile*, suggesting that it lies closer to the stem campaniloidean than *Campanile*. Ponder (1991b) used *Campanile* as an outgroup to the Cerithioidea in his analysis of cerithioidean relationships.

Inclusion of the Plesiotrochidae within the Campaniloidea on the basis of eusperm and parasperm synapomorphies (see Healy 1993b) poses the problem of re-defining the Campaniloidea. Given the enormous differences between *Campanile* and *Plesiotrochus* not only in size (shell up to 244 mm in *Campanile*, rarely exceeding 10 mm in *Plesiotrochus*), but also in habitat (on weed among rocks for *Campanile*, on seagrass for *Plesiotrochus*) it is perhaps not surprising that there should be several anatomical differences between these genera. The following provisional diagnosis, can however, be proposed here for the Campaniloidea, combining shared features of the two families based on available data.

Revised diagnosis of the Campaniloidea: Shells turreted with the upper portion of whorls usually straight or slightly concave (sometimes convex) and variously sculptured with spiral cords (sometimes developed as low nodules) or rarely varices; short anterior siphonal notch present; operculum rounded to quadrate, paucispiral, with the nucleus slightly eccentric; periostracum usually well developed, often thick or hairy; head-foot with short, snout (slightly bilobed at tip); cephalic tentacles pink, short to elongate; head and mantle edge often pink or mottled with pink; ctenidium large and monopectinate; osphradium ovate and bipectinate (either entirely or at least in the posterior half); radula taenioglossate with rachidian featuring central cusp and lateral cusps on cutting edge and broad basal plate, laterals and marginals curved to hooked with prominent terminal cusps; usually hermaphroditic, either simultaneously or protandrically; gonoducts are open and a penis is absent; spermatozoa are of two principal types: (1) euspermatozoa featuring a midpiece composed of 7 or 8 straight mitochondrial elements (with random

cristae), an axoneme and a uniquely segmented midpiece sheath; (2) paraspermatozoa – anucleate type with acrosome-like structure, head region (dense vesicles surrounding core of mitochondria and 2 or 3 axonemes) and flagella tuft (2 or 3 flagella), nucleate type (co-occurring with anucleate type in *Campanile*, ? present also in *Plesiotrochus*) similar but with nuclear core replacing mitochondria as axial component of parasperm ‘head’ region.

Most of the differences between the campaniloidean families (aside from physical size differences) involve the organisation of the nervous system and details of the digestive system (stomach structure and the position of the salivary glands relative to the nerve ring).

Family Campanilidae

The large and remarkable Australian species, *Campanile symbolicum*, was most often placed in the family Cerithiidae because of its cerithiid-like shell. Houbbrick (1981a) investigated the anatomy and biology of the species and concluded that it belonged in the Cerithioidea, but should be placed in a separate family, the Campanilidae, because of its unique shell and anatomical characteristics.

The shell of *C. symbolicum* is large (up to 244 mm long), with 25 to 30 flat-sided whorls, is usually decollate, and has a weak keel at the base (Fig. 15.98A). A row of low nodules is sometimes well developed on the juvenile whorls of the shell (Fig. 15.98B), but more frequently such nodules are only faintly visible or absent. The outer shell is off-white with a chalky periostracum and the aperture is relatively narrow and angulate, with a distinct anterior siphonal canal. In mature specimens the outer lip sweeps backwards in a broad sinus. The uppermost whorls of the shell of juveniles and adults are sealed off, and not occupied by tissue. The protoconch is smooth, bulbous, composed of one and a half whorls and lacks a sinusigeral notch. The operculum is brown, paucispiral and corneous (Fig. 15.98C; Houbbrick 1981a, 1984d, 1989).

The following summary of the anatomy of *Campanile symbolicum* is based primarily on Houbbrick’s studies (1981a, 1984d, 1989). The head-foot is white to flesh coloured, but is bright pink in sexually mature animals, and has a short, broad snout (bilobed at extremity) and a pair of short pink cephalic tentacles with a eye positioned at the base of each tentacle (Fig. 15.98D). The glandular periphery of the sole produces mucus and is considered by Houbbrick to be an extension of the anterior pedal gland. A long, strap-like columellar muscle enables deep retraction into the shell which is an effective defence mechanism (Houbbrick 1981a). The mantle cavity (Fig. 15.98D, E) contains, among other structures, a large, bipectinate osphradium (brown in colour, elongate-oval in shape; for ultrastructural details see Haszprunar 1992b); a long, pink ctenidium (running almost the full length of the mantle cavity); a long, well-developed hypobranchial gland (again extending the length of the mantle cavity); an open, glandular pallial gonoduct; a renal organ; a thick rectum (faecal pellets composed of detrital material); and a gonoduct. The jaws are thick and curved, with a four-layered substructure; the buccal mass is rounded and supported by well-developed odontophoral cartilages. Each tooth row of the radula (Fig. 15.98I) has a broad central tooth with a large central cusp flanked on each side by a poorly developed small cusp and a concave basal plate, each side showing a small denticle. The strong lateral teeth have a pronounced triangular cusp flanked by a small inner cusp and a small outer cusp. The curved, terminally hook-shaped marginal teeth have sharp tips and a small inner cusp; the marginal tooth base is spatulate. A pair of salivary glands lie anterior to, but not passing through, the nerve ring. A pair of muscular buccal pouches lies close to the salivary glands, also anterior to the nerve ring. The oesophagus leads to a large and structurally complex stomach which, although having a style sac, has no crystalline style, only a protostyle. Other notable features of the stomach include a cuticularised, grooved sorting area and glandular, spiral leaflets. The nervous system features long connectives between the cerebral ganglia, a suboesophageal

ganglion close to the pleural ganglion and long cerebropedal connectives. Zygoneury is present. Animals are probably protandrous hermaphrodites; the open pallial gonoduct of ‘females’ is larger and more glandular than that of ‘males’. Euspermatozoa are of campaniloidean type; paraspermatozoa are dimorphic (i.e. with or without nuclear core), posteriorly flagellate (usually only two tails) (Fig. 15.98F, G; Healy 1986a, 1986b, 1996). The eggs are laid in a large, crescentic, gelatinous mass (Fig. 15.98H) which is attached to firm substrata (rocks, seagrasses, macroalgae) in the spring, from September through November (Houbbrick 1981a). Each egg mass measures, on average, about 175 mm in length, 21 mm in width, and 5 mm in thickness, and contains approximately 4000 pink eggs. Between one to three (sometimes five) eggs are packaged in mucus-walled egg chambers which in turn are linked by threads to other chambers to form a continuous, spiral strand within the egg mass (Houbbrick 1981a). The young are thought to undergo either a short veliger stage or to be released as crawling young; Houbbrick (1981a) reported finding advanced veligers with a shell of one and a half whorls and favoured the conclusion that development is direct.

Campanile symbolicum is common and conspicuous within its range in southern Western Australia (from the Recherche Archipelago, east of Esperance to Geraldton) where it lives in shallow (1–4 m depth) subtidal sandy habitats, often in sand and weed pockets among rocks. According to Houbbrick (1981a) this species appears to be most active at night, possibly a strategy to reduce predation. Although *C. symbolicum* has been the subject of recent anatomical and ultrastructural studies (Houbbrick 1981a, 1984d, 1989; Healy 1986b; Haszprunar 1992b) much remains to be learned of its ecology and aspects of reproductive biology. Currently *C. symbolicum* is the focus of international attention by malacologists attempting to resolve the phylogeny of prosobranch gastropods, especially the origins and relationships of the Caenogastropoda. Such interest stems from the unique mix of anatomical features of this species which suggests connections with the Cerithioidea on the one hand and on the other hand with other neotaenioglossans and the Neogastropoda. However, with the addition of the Plesiotrochidae to the Campaniloidea, many of the features of *C. symbolicum* may now be considered as characteristic of the Campanilidae alone rather than of the entire Campaniloidea. Possibly other, as yet unrecognised, campaniloidean taxa await discovery. *Campanile symbolicum* is the sole survivor of a family once widespread in the Tethys Sea. The almost total demise of the family during the late Eocene and early Miocene may have been associated, as suggested by Houbbrick (1981a), with trophic and ecological competition from the Strombidae.

Three subgenera of *Campanile* were recognised by Delpy (1941): *Diozoptyxis* (extinct), *Campanilopa* (extinct) and *Campanile* (*sensu stricto*) (extinct with exception of *C. symbolicum*). According to Houbbrick (1981a), New World fossil campanilids are contained within the genus *Dirocerithium*, whereas *Campanile sensu stricto* contains fossils from Europe, Java and Australia. *Campanile symbolicum* is known from the Pleistocene of Western Australia (Houbbrick 1981a) and the early Pleistocene and Holocene of the Eucla Basin, South Australia (Ludbrook 1978). Ludbrook (1971) noted two other fossil species of *Campanile* from Australian deposits – *C. triseriale* and *C. virginense*, both from the Upper Pliocene of South Australia. Another possible fossil species of the genus, from Western Australia, mentioned by Ludbrook, is known only from casts and moulds.

Family Plesiotrochidae

The small Indo-West Pacific family Plesiotrochidae is represented by the single genus *Plesiotrochus* (= *Hemicerithium*, *Trochocerithium*, *Hypotrochus*) with about a dozen nominal species (Houbbrick 1990b) all of which are small (shell length 10 mm or less, exceptionally up to 20 mm). Wilson (1993) listed the following five species of *Plesiotrochus* in Australia: *P. crinitus*, *P. souverbianus*, *P. pagodiformis*, *P. acutangulus* and

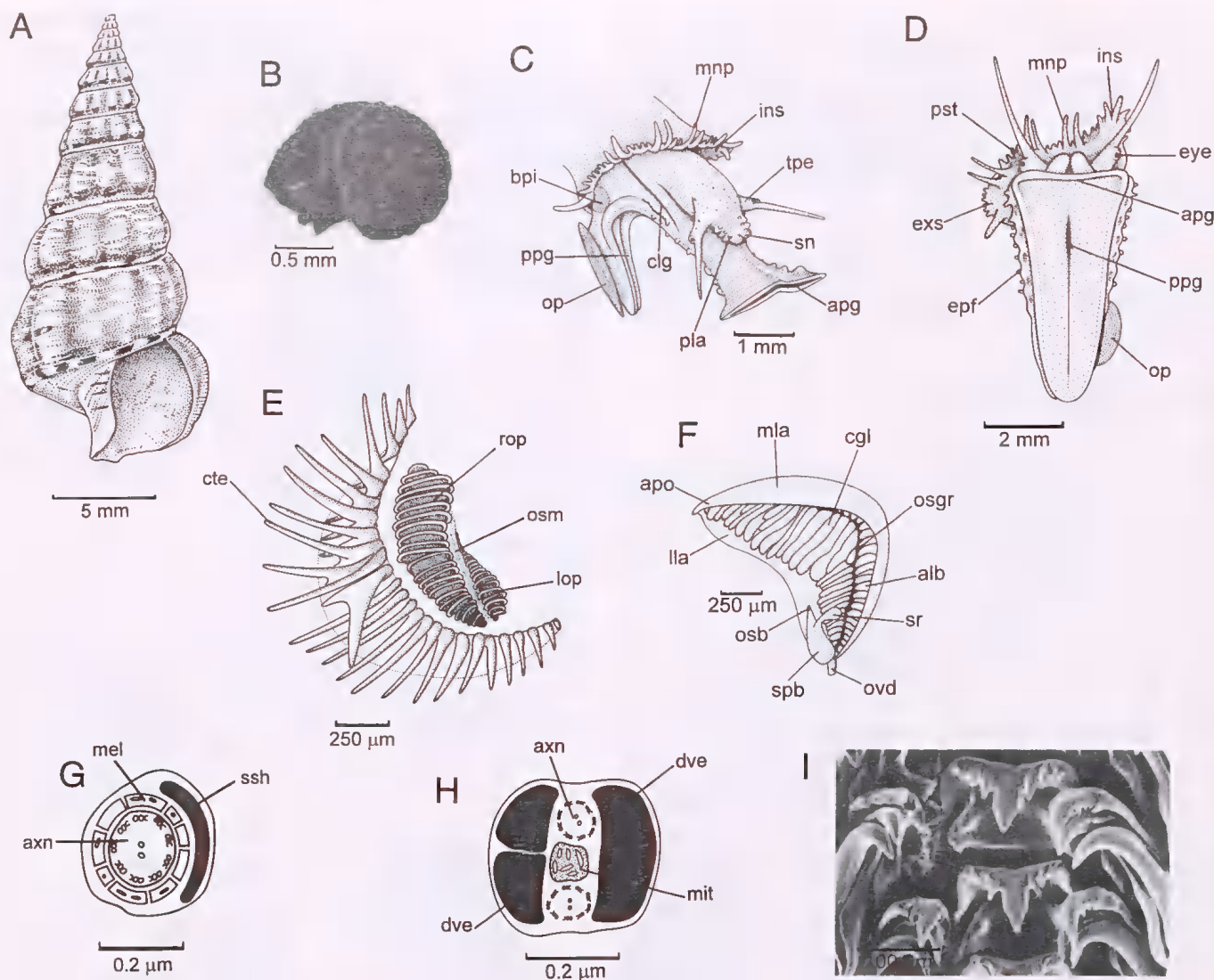


Figure 15.99 Family Plesiotrochidae. **A**, *Plesiotrochus monachus*, shell, apertural view. **B–I**, *Plesiotrochus crinitus*: **B**, operculum; **C**, head-foot showing details of snout, foot and mantle edge; **D**, animal, ventral view, showing details of the sole of the foot; **E**, details of the osphradium (note bipectinate morphology posteriorly) and ctenidium; **F**, pallial gonoduct and associated organs and glands; **G**, cross section of euspermatozoon through 'head' region; **H**, cross section of paraspermatozoon through midpiece region; **I**, portion of radula, showing central and lateral teeth. **alb**, albumen gland; **apg**, anterior pedal gland; **apo**, anterior pallial oviduct; **axn**, axoneme; **bpi**, brown pigment; **cgl**, capsule gland; **clg**, ciliated groove; **cte**, ctenidium; **dve**, dense vesicle; **epf**, epipodial fringe; **exs**, exhalant siphon; **eye**, eye; **ins**, inhalant siphon; **lla**, lateral lamina; **lop**, left osphradial pecten; **mel**, mitochondrial elements; **mit**, mitochondrion; **mlla**, medial lamina; **mnp**, mantle papillae; **op**, operculum; **osb**, opening of spermatophore bursa; **osgr**, oviductal/spermiductal groove; **osm**, osphradial membrane; **ovd**, coelomic oviduct; **pla**, papilla; **ppg**, posterior pedal gland; **pst**, pigmented spot; **rop**, right osphradial pecten; **spb**, spermatophore bursa; **sn**, snout; **sr**, seminal receptacle; **ssh**, segmented sheath; **tpe**, tentacular peduncle. (**B**, **I**, from Houbbrick 1990b; **C–F**, after Houbbrick 1990b; **G**, **H**, after Healy 1993b) [A, R. Plant; C–H, C. Eadie]

P. monachus. Although plesiotrochids occur in other areas of the Indo-West Pacific (Houbbrick 1990b), more species occur in Australian waters than elsewhere. Plesiotrochids can be distinguished from the Campanilidae and cerithioidean families by the following combination of features: a small, trochiform (often pagoda-like) shell; a narrow snout; short, wide cephalic tentacles with long peduncular lobes; very thick jaws; a thin epipodial fringe that completely surrounds the foot; a median posterior pedal gland; a large propodium; a deep anterior pedal gland; short to long, well-developed papillae on the dorsal surface of the mantle edge; a distinctive osphradium (anterior portion monopectinate, posterior bipectinate); simultaneous hermaphroditism (confirmed at least in *P. crinitus*) (Houbbrick 1990b).

The plesiotrochid shell (Fig. 15.99A) is trochiform to pagodiform, usually small (5 mm, but ranging up to 20 mm in *P. monachus*) and has an angulate aperture with an anterior siphonal notch. The whorls are often stepped in a pagoda-like fashion and flat to concave, but may be convex and show varices in some species (for example, *P. monachus*). The protoconch may be small with a sinusigeral notch, or large and bulbous and lacking sculpture or a notch. The periostracum is usually thin and hairy and very thick in some species. In all species, the operculum is ovoid, paucispiral with an eccentric nucleus (Fig. 15.99B; Houbbrick 1990b).

The head-foot is warty, often coloured, with a prominent pair of cephalic tentacles associated with large eyes set on long peduncular bases (Fig. 15.99C, D). The foot is narrow and, according to Houbbrick (1990b), prehensile, enabling the animal to grip firmly on the algal strands. Rapid movement and emergency anchorage are also facilitated by the well-developed anterior and posterior pedal glands (the latter being capable of producing a mucous thread in case of dislodgment of the animal). Within the mantle cavity are contained the osphradium (bipectinate posteriorly – Fig. 15.99E); ctenidium (with elongate filaments, reinforced by rods – Fig. 15.99E), hypobranchial gland; rectum (with ovoid faecal pellets); and covering the posterior portion of the pallial gonoduct, the renal organ (Houbbrick 1990b). Each tooth row of the radula (Fig. 15.99I) has a central tooth with a prominent central cusp flanked on each side by three smaller cusps, and a hourglass-shaped basal plate, featuring a pair of lateral extensions and a pair of lateral denticles. The lateral teeth are long with a prominent central cusp, two to three small inner cusps and three small outer cusps. The marginal teeth are curved with hook-shaped tips bearing a large cusp and variable number of smaller cusps (the latter absent in outer marginal teeth) (Houbbrick 1990b). Salivary glands are elongate, paired and pass through the nerve ring. The oesophagus is not associated with an oesophageal gland and leads to a large stomach containing sorting ridges, style sac and gastric

shield (Houbrick 1990b stated that he observed no crystalline style – possibly indicating dissolution). The nervous system features long connectives between the cerebral ganglia, between the suboesophageal ganglia and the left pleural ganglion and between the right pleural ganglion and supra-oesophageal ganglion. Plesiotrochids are probably all simultaneous hermaphrodites if *P. crinitus* is typical of the family. Houbrick (1990b) found that in this species the gonad is divisible into testis and ovary zones, both actively producing sperm and oocytes respectively (see also Healy 1993b). The pallial gonoduct (Fig. 15.99F) is heavily glandular, with regions interpretable as albumen gland and a probable egg capsule gland. Euspermatozoa and paraspermatozoa of *P. crinitus* closely resemble those of *Campanile symbolicum* (Fig. 15.99G, H; Healy 1986a, 1986b, 1993b).

Information on habitat is available for only three species: *Plesiotrochus monachus*, *P. souverbianus* and *P. crinitus* (Houbrick 1990b; *P. crinitus*, discussed and figured under the name *P. cf. penitricinctus* by Houbrick). *Plesiotrochus crinitus* was found on brown algae in a sheltered pool on a rocky shore. The animals are active and in the laboratory exhibited pseudocopulation with the release of spermatophores. They are simultaneous hermaphrodites with discrete male and female sections in the gonad. Protoconch morphology suggests that development is probably direct in *P. monachus* (large, bulbous protoconch) and probably indirect in *P. souverbianus* (protoconch small, with sinusigeral notch) (Houbrick 1990b). According to Ludbrook (1984), *P. monachus* is found in large numbers on algae on silty bottoms, or sometimes on *Posidonia* seagrass, at 5–20 m, and is especially common at Outer Harbor, South Australia. Species of *Plesiotrochus* are algal feeders. Hedley (1907) mentioned that his species, *P. pagodiformis*, occurred at depths of 31–37 m off Mast Head Island (Queensland) but did not provide any information on its habitat.

The genus *Plesiotrochus* has been placed at various times in the Littorinidae, Planaxidae and Cerithiidae because, aside from Hedley's (1907) figures of the radula and operculum of *P. monachus*, no other anatomical information was available. Houbrick (1990b), however, has provided a detailed study of preserved and living *Plesiotrochus*. His work was based primarily on *P. crinitus* (as *P. cf. penitricinctus*) from southern Western Australia and preserved material of *P. monachus* and *P. souverbianus*. Certain anatomical features such as the open pallial gonoducts, absence of a penis, and the presence of two pouches on the gonoduct (possible bursa copulatrix and a seminal receptacle), were thought by Houbrick (1990b) to establish definitively the cerithioidean status of *Plesiotrochus*. Nevertheless, Houbrick also pointed out a number of other characters which are uncommon or do not occur in other cerithioidean families such as a pinched narrow snout; short, wide cephalic tentacles with long peduncular lobes; very thick jaws; a thin epipodial fringe which completely surrounds the foot; a median posterior pedal gland; a large propodium; a deep anterior pedal gland; short to long, well-developed papillae on the dorsal surface of the mantle edge; a distinctive osphradium in which the anterior portion is monopectinate but the posterior is bipectinate and large; and simultaneous hermaphroditism (confirmed at least in *P. crinitus*). The anatomical distinctiveness of *Plesiotrochus* species led Houbrick (1990b) to erect the new family Plesiotrochidae. This decision is supported by sperm data, which in addition clearly indicate a close relationship of the Plesiotrochidae and Campanilidae (Healy 1993b). Both Thiele (1929–1935) and Cotton (1960) had already associated plesiotrochids (only some for Thiele) and campanilids in the cerithiid subfamily Campanilinae.

According to Ludbrook (1984), the extant species *Plesiotrochus monachus* occurs in Late Pleistocene and Holocene (Recent) sediments of South Australia (Glanville and St Kilda formations, respectively). Whether the Pliocene fossil species, *Hypotrochus semiplicatus* described by Ludbrook (1957) actually belongs within the Plesiotrochidae requires confirmation.

Infraorder LITTORINIMORPHA

This group comprises the 'higher mesogastropods', encompassing taenioglossate hypsogastropods (excluding the taenioglossate ptenoglossans). As outlined below, it has some distinctive sperm ultrastructural features separating it from the Cerithioidea and Campaniloidea. This large and very diverse group contains many of the familiar marine gastropods but relationships within the group have received very little attention. Shell forms range from high-spired and tightly coiled, to limpets and uncoiled tubes and a few (Velutinidae) have slug-like bodies. Most littorinimorphs are marine but several groups have invaded freshwater and a few the land. Because there is no modern phylogenetic treatment available including most members of this group, it remains unclear as to whether or not it is paraphyletic with respect to the Neogastropoda and Ptenoglossa.

It is partially equivalent to the paraphyletic Mesogastropoda of Thiele (1929–1935) and Neotaenioglossa and Discopoda + Heteropoda of Ponder & Warén (1988) but excludes Cerithioidea, Ptenoglossa and Campaniloidea.

Superfamily LITTORINOIDEA

Members of this superfamily may be marine, freshwater or terrestrial and are small to medium in size, with rather simple shells having an entire peristome and lacking an inner organic layer. A penis is present in males. The group consists of three closely related families, the mainly marine Littorinidae, the Zeratulidae (recently described by Warén & Hain 1996) and the terrestrial Pomatiasidae; two families of doubtful affinity, the Northern Hemisphere family Skeneopsidae (see Fretter 1948 for anatomical and biological details) and the poorly known Pickworthiidae, are also tentatively included here. The relationships and definition of the superfamily have been discussed by Ponder (1988a), Reid (1989a) and Warén & Hain (1996). The family Eatonellidae, originally included here, is now placed in the superfamily Cingulopsoidea.

The following diagnosis is based on the Littorinidae, Zeratulidae and Pomatiasidae. The shells are up to 50 mm in height and turinate, trochoidal or conical, sometimes smooth, but usually have spiral sculpture, or are nodulose. The operculum is corneous or calcified, paucispiral or multispiral. The head bears a pair of tentacles with eyes on swellings at their bases, the snout is broad and short and neck lobes are absent. Pallial and metapodial tentacles are absent and locomotion is typically ditaxic. A posterior pedal gland is present only in Zeratulidae. Littorinoideans are herbivorous grazers and the radula is long, narrow and taenioglossate. Oesophageal pouches and oesophageal glands are present in the Littorinidae and Zeratulidae, and a crystalline style in the stomach of the Pomatiasidae. The monopectinate ctenidium is reduced or lost in terrestrial representatives. Almost all littorinoideans are gonochoristic. Reproductive anatomy varies widely. Pallial gonoducts may be open or closed in both sexes. Males have a penis on the right side of the head, with innervation wholly from the pedal ganglion (Littorinidae) or from pedal and suboesophageal ganglion (Zeratulidae, Pomatiasidae). Sperm are sometimes dimorphic. The bursa copulatrix may be anterior, posterior or absent, and sperm may be stored in a seminal receptacle, the oviduct, ovary or pericardium. The life cycles show a wide range from planktotrophic to nonplanktotrophic and ovoviparous forms.

The Pomatiasidae are terrestrial, and occur in the American tropics (the subfamily Annulariinae, sometimes referred to as Chondropomatinae, is sometimes given familial status), and in Europe, Africa and Asia, but are not represented in Australia. The marine Zeratulidae have so far been recorded only from the Antarctic, New Zealand, New Caledonia, and the North Atlantic, mostly in deep water; zeratulids may well be found off Australia. The Littorinidae are marine or rarely freshwater, with a worldwide distribution. Two additional marine families, Skeneopsidae, found only in the Northern Hemisphere, and the Pickworthiidae, are tentatively included in this superfamily.

15. PROSOBRANCHS

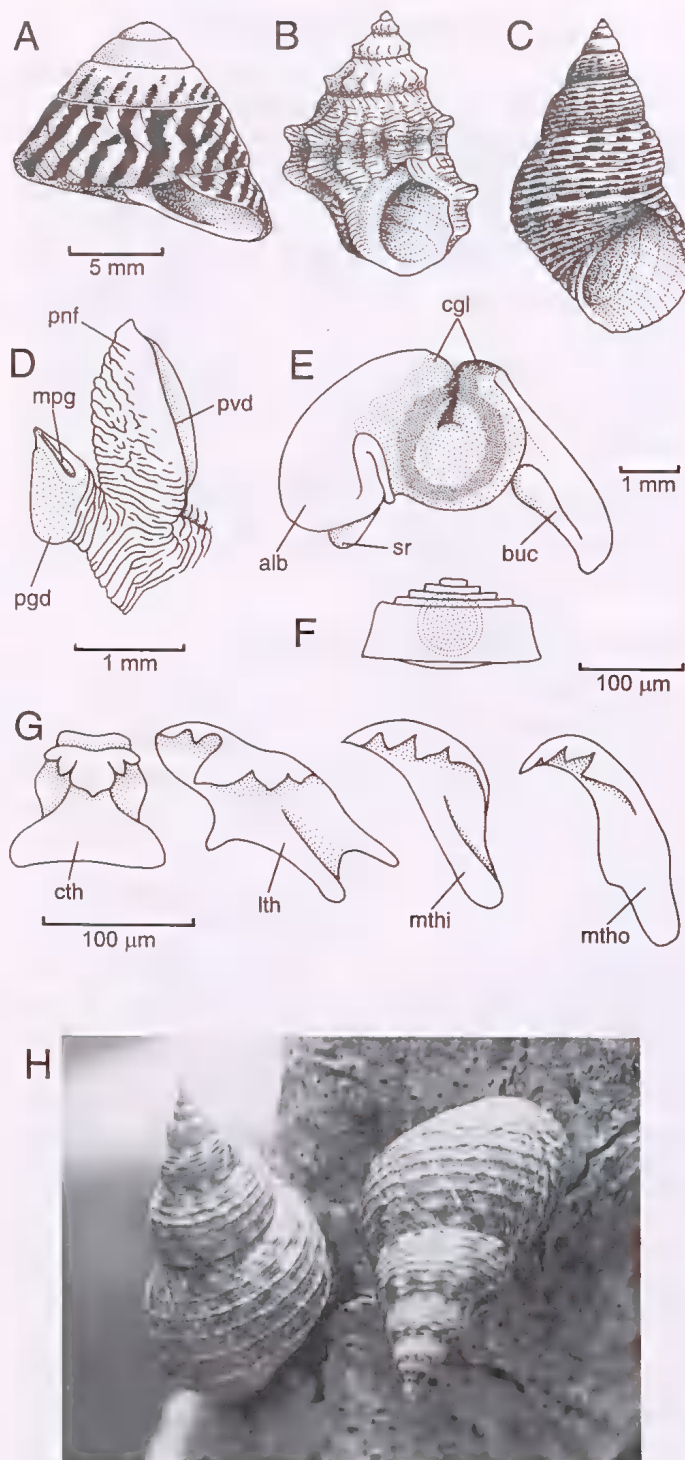


Figure 15.100 Family Littorinidae. A–C, shells, apertural view: A, *Bembicium nanum*; B, *Nodilittorina pyramidalis*; C, *Littoraria luteola*. D, penis of *Nodilittorina unifasciata*. E, pallial oviduct of *Nodilittorina pyramidalis*. F, egg capsule of *Nodilittorina* sp. G, *Littoraria scabra*, half a transverse row of radular teeth. H, *Littoraria philippiana* is commonly found in tropical and subtropical Australia on the trunks of mangrove trees. buc, bursa copulatrix; cgl, capsule gland; cth, central tooth; lth, lateral tooth; mpg, mammilliform penial glands; mthi, marginal tooth, inner; mtho, marginal tooth, outer; pgd, penial glandular disc; pnf, penial filament; pvd, penial vas deferens (open groove); sr, seminal receptacle.

[A–G, D.G. Reid; H, L. Newman & A. Flowers]

Family Littorinidae

Members of this worldwide family are commonly known as winkles or periwinkles, and are most frequently found on hard substrata in the littoral fringe. The shells are small or medium in size, and turbate to conical. Anatomically, the family is defined by the complex looped or spiralled form of the egg groove in the closed pallial oviduct, which usually has an anterior bursa copulatrix.

Traditionally, the classification of the Littorinidae has been based on a combination of shell and radular features (see for example, Rosewater 1970, 1972). More recent work has emphasised characters of the reproductive anatomy, of sperm and of egg capsules, leading to a revision of generic definitions (Bandel & Kadolsky 1982; Reid 1986b, 1989a) and to the recognition of many more species. A supraspecific classification based on a cladistic analysis of morphological data (Reid 1989a) is now generally followed. At the specific level, the taxonomy of the Australian species is well known, and most have been included in monographs of *Nodilittorina* (Rosewater 1970, but see modifications by Reid 1989a, 1992a), *Tectarius* (Rosewater 1972), *Littoraria* (Reid 1986b), *Bembicium* (Reid 1988) and *Peasiella* (Reid 1989b). The species now included in *Laevilittorina* (Reid 1989a) were described by Ponder (1976) and Ponder & Rosewater (1979). General accounts of littorinid anatomy have been given by Fretter & Graham (1962) and Reid (1989a). Owing to the abundance and accessibility of these snails, they have been the subject of a large volume of research on ecology, behaviour, physiology and genetics (for reviews, bibliographies and recent research see Pettitt 1974; Underwood 1979; Raffaelli 1982; Reid 1986b, 1988, 1989a, 1996; Johannesson, Raffaelli & Hannaford Ellis 1990; Grahame, Mill & Reid 1992; Mill & McQuaid 1995). Most of this work has been carried out on European species, but much is also known about the community ecology of some Australian species.

The following morphological description is based on the review by Reid (1989a). The shells are 2–50 mm in height, solid, turbate to conical or trochoidal, usually spirally grooved, or sometimes nodulose or spinose, and generally imperforate (Fig. 15.100A–C). Colouration is variable, often consisting of axial stripes; species found on mangrove foliage are polymorphic brown, yellow and red. In species with planktotrophic development, the protoconch is 0.21–0.44 mm in length, of two to four whorls, sculptured by tubercles or spiral ribs, and terminated by a strong sinusigeral rib. In nonplanktotrophic species (and in secondarily planktotrophic *Bembicium* species), the protoconch is smooth, larger, of fewer whorls and less clearly differentiated from the adult shell. The aperture is rounded, oval or quadrate, and the peristome entire. The operculum is usually corneous, paucispiral, and ear-shaped, with an eccentric nucleus, but is sometimes multispiral with a central nucleus, and rarely calcified.

In all marine species, the anterior pedal gland opens into the transverse propodial groove; a posterior pedal gland is absent. Locomotory waves on the sole of the foot are retrograde ditaxic, and a median longitudinal groove is usually visible. Opercular lobe tentacles are present only in species of *Lacuna* and one species of *Laevilittorina*.

Littorinids graze on algal films, macroscopic algae, and epiphytic growths and leaf hairs on mangrove trees (Fig. 15.100H). The radula is a half to eight times the length of the shell and is coiled over the mid-oesophagus. The central tooth is square to rectangular, usually with five cusps, but sometimes reduced to a narrow rod; the lateral is large, quadrate, with a postero-lateral notch in the base, usually with one to two principal cusps and several smaller cusps; the inner marginal is narrower, with one to five cusps, and the outer marginal commonly slender with one to ten cusps (Fig. 15.100G). There is no jaw. The ducts of the single pair of salivary glands usually pass through the circum-oesophageal nerve ring, but the glands may be entirely anterior to or constricted by the nerve ring; a pair of oesophageal pouches (often called buccal pouches) is present anterior to the nerve ring, and the mid-oesophagus is glandular. The stomach is often elongate, with a style sac and gastric shield, but no crystalline style. Within the mantle cavity there is a monopectinate ctenidium, a hypobranchial gland and an elongate, simple osphradium; the gill lamellae are reduced in size in *Littoraria* and other high-shore species.

Littorinids are almost all gonochoristic, but the two *Mainwaringia* species are protandrous hermaphrodites. Males are recognisable by the conspicuous penis (Fig. 15.100D) below and behind the right cephalic tentacle, which commonly bears discoidal and/or mammilliform appendages with subepithelial mucous glands. The form of the penis is of crucial importance in the species-level taxonomy of most genera, since shell characters can be rather variable. In some species regression of the reproductive organs takes place outside the breeding season, and may also be caused by trematode parasites. Sperm pass along the penis in an open groove or a closed tube. The prostate is commonly open, but is sometimes closed. Sperm are dimorphic in the subfamily Littorininae; typical euspermatozoa are thread-like, and attached in bunches to the paraspermatozoa (or nurse cells), which are rounded and contain granules, rods and sometimes a long cytoplasmic extension. In females of oviparous species, an ovipositor is present on the side of the head. The pallial oviduct is closed and monaulic (Fig. 15.22C). A large, muscular, bursa copulatrix for the reception of sperm is usually present near the anterior end of the pallial oviduct, but is occasionally absent, and there is a seminal receptacle for sperm storage at the posterior end (absent in some Lacuninae). The dorsal egg groove in the pallial oviduct follows a complex path of loops and spirals, along which albumen, capsule and jelly glands of epithelial or subepithelial tissues are differentiated (the last two are sometimes absent).

Life histories show considerable variation in the Littorinidae, and much can now be deduced about the evolution of spawn types and of larval development (Reid 1989a, 1992b). Primitively, littorinids produce benthic gelatinous spawn masses containing unencapsulated eggs. In the subfamilies Laevilitorininae and Lacuninae, development is usually nonplanktotrophic, and takes place within the egg mass (probably as an adaptation to cold water), although probable reversion to planktotrophy has occurred in three genera (including some species of *Bembicium*). In the more highly derived subfamily Littorininae, the eggs are mostly pelagic, enclosed singly in ornately sculptured capsules (Fig. 15.100F) that are produced by a new gland in the pallial oviduct, and this may have been one of the most important adaptations permitting their colonisation of the littoral fringe. These pelagic eggs undergo planktotrophic development, which is primitive in the family as a whole. Only in some cold-water *Littorina* species has the spawn become benthic once more, and in these development is nonplanktotrophic, in one species with ovoviviparity. A few tropical species of *Littoraria* also brood embryos, but usually release planktotrophic veligers. Accounts of larval development have been given by D.T. Anderson (1962) and Struhsaker & Costlow (1968).

With the exception of one freshwater genus (the Indian *Cremnoconchus*) and the mainly sublittoral and eulittoral members of the Lacuninae and Laevilitorininae, most littorinids occupy the littoral fringe. The habitat and zonation of littorinids on rocky shores in Australia have been described in general accounts of intertidal zonation (for example, Knox 1963; Underwood 1981) and of the mangrove-dwelling species by Reid (1985). Most ecological work on littorinids in Australia has involved the common species of *Nodilittorina* and *Bembicium* on temperate rocky shores, and will be reviewed briefly. The reproductive cycles of three species at Sydney have been documented by Underwood (1974). Maturity is usually reached in one year, maximum size in two to three years, and longevity may be up to eight years in larger species (Underwood 1975a; Underwood & McFadyen 1983; Wells 1984). Caging experiments have demonstrated intra- and interspecific competition for food in these littorinids, which often occur at very high densities (Underwood 1978, 1984; Branch & Branch 1980b, 1981). There have been a number of studies of movement and dispersal of species in New South Wales (Underwood 1975b, 1976a; Underwood & Chapman 1989, 1992; Chapman 1994a, 1994b, 1995b). Predation by crabs has been examined for *Bembicium* (Chilton & Bull 1984, 1986) and in tropical mangrove-dwelling *Littoraria* (Reid 1992c). Although there is much information on the population genetics of northern Atlantic species (Ward 1990), the allozyme studies by Johnson & Black (1991, 1995, 1996) on *Bembicium* are the first of

this kind in Australia. Selection mechanisms which may promote the colour polymorphism of mangrove-dwelling *Littoraria* species have been investigated by J.M. Hughes & Mather (1986) and Reid (1987). Since most of the Australian species are planktotrophic and therefore widely dispersed, they do not show such marked intraspecific variation in shell shape as some European *Littorina*, but local variation has been described by McMahon (1992) and Chapman (1995a). Thermal tolerance and water loss have been measured in high-shore Australian littorinids (McMahon 1990, 1991; McMahon & Britton 1991), and the adaptive significance of shell form in this environment has been discussed by Vermeij (1973).

The family Littorinidae contains 13 genera and about 180 species, grouped in three subfamilies, Lacuninae, Laevilitorininae and Littorininae. This classification is based on a phylogeny of all 33 recognised subgenera, produced by cladistic analysis of morphological data (Reid 1989a). The basal group Lacuninae is of bipolar distribution and includes the freshwater Indian *Cremnoconchus*. The Lacuninae are represented on the Australian mainland by four species of the endemic Australasian genus *Bembicium* (*B. auratum*, *B. nanum*, *B. melanostoma*, *B. vittatum*). The Laevilitorininae, containing the single genus *Laevilitorina*, are an Antarctic group, but four endemic species occur in southern Australia. The typical winkles of the littoral fringe are members of the Littorininae, of worldwide occurrence mainly on tropical, but also temperate, coasts. This subfamily is represented in Australia by four species of *Peasiella*, one *Tectarius*, 11 *Littoraria* and nine *Nodilittorina* (the familiar genus *Littorina* does not occur outside the Northern Hemisphere and southern Africa). Many of the northern and north-eastern Australian species of Littorininae are widely distributed in the Indo-Pacific province, whereas the temperate species (*N. australis*, *N. praeterrissa*, *N. acutispira*, *N. unifasciata*, *N. pyramidalis sensu stricto*, *Littoraria luteola*) and some in the north-west (*T. rusticus*, *Littoraria cingulata*, *L. sulculosa*) are endemic. Distribution maps of most of the 33 littorinids can be found in the taxonomic monographs listed earlier.

The fossil record of Littorinidae is sparse, because of poor preservation in their largely littoral habitat, and due to the difficulty of recognising members by their shells. The oldest undoubted littorinids are recorded from the Palaeocene of Europe and California. Only a single fossil species (*Bembicium altum*) has been recorded from Australia (Tate 1893a).

Family Pickworthiidae

Members of the marine Pickworthiidae have small shells, with an adult height range of 0.5–5 mm (Fig. 15.101). The shell is white, highly variable, ranging from planispiral to tall and slender, with a height/maximum diameter ratio from 0.3 to 3. The aperture is circular, prosoclinely oblique, bordered by a thickened pad, formed by successive layers of peristome. An umbilicus may be present or absent. The protoconch and teleoconch often have different coiling axes, the protoconch appearing obliquely inclined on the apex of the adult shell. The protoconch is light brown, generally of planktotrophic type, consisting of two convex whorls, sculptured by two to ten granular spiral cords, ending in a deep sinusigeral notch (Fig. 15.101G).

Empty shells are not uncommon at subtidal depths in the tropical Indo-Pacific and Atlantic regions, but only a few live-taken specimens have so far been collected (in deep crevices on the outer slope of the barrier reef in New Caledonia and in dark caves throughout the West and South Pacific). Consequently, nothing is known of the anatomy, ecology or biology of the family. A parasitic way of life may possibly be inferred from the apertural shield and tubes of *Sherbornia mirabilis*, but this is purely conjectural.

Protoconch morphology indicates a probable position in the Cerithioidea or Littorinoidea, and the superfamilial placement requires confirmation, pending knowledge of the anatomy.

15. PROSOBRANCHS

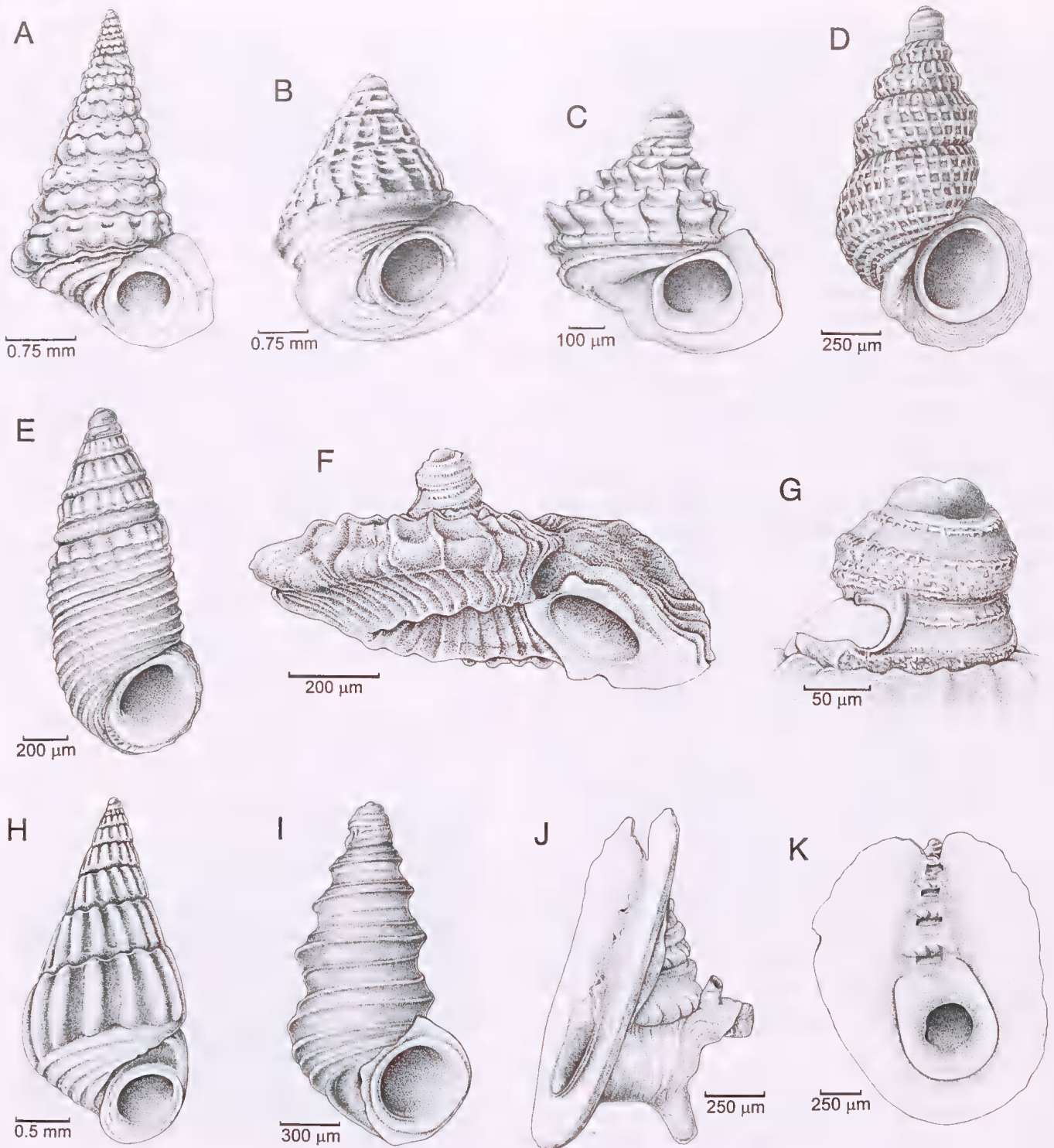


Figure 15.101 Family Pickworthiidae. A, *Sansonia kirkpatricki*, Christmas Island. B, *Microliotia saturnia*, Euston Reef, Queensland. C, *Mareleptopoma spinosa*, West Ngalignagho Island, Solomon Islands. D, *Clatrosansonia minuta*, Swains Reef, Queensland. E, *Discrevinia balba*, Carter Reef, North Queensland. F, G, *Astrosansonia dautzenbergi*, Tuamotu Island, French Polynesia. H, *Reynellona natalis*, off North East Point, Christmas Island. I, *Chrystella finckhi*, Kira-el-Kurtinai, Egypt, Red Sea. J, K, *Sherbornia mirabilis*, Mururoa, Tuamotu Island, French Polynesia. A–E, F, H, I, shells, apertural view; G, protoconch; J, shell, lateral view; K, shell, dorsal view. [C. Vachetot]

The Pickworthiidae and its synonyms, Reynellonidae and Sherborniidae (introduced simultaneously by Iredale in 1917a) were all described on the basis of species from Christmas Island (Indian Ocean), in an unusually rich sample taken by R. Kirkpatrick in 100 fathoms. The family is known to contain 10 genera (nine Recent) and 50 species (36 Recent). All Recent genera and 16 species are presently recorded from Australian waters (Western Australia, Queensland and Christmas Island). The absence of records from the Northern Territory is certainly a sampling artefact. Given their small size, more species undoubtedly await discovery. One species is possibly an Australian endemic.

Sansonia (= *Mecoliotia*, = *Pickworthia*) is the type genus of the family. It is characterised by a trochoid teleoconch, with one to four spirally arranged rows of nodules, a flat base and a thick projecting outer lip. Four species are recorded from Australia. Of these, *S. kirkpatricki* (Fig. 15.101A) and *S. andamanica* (= *andrewsi*) are common in coral sand from the Great Barrier Reef. *Microliotia* differs from *Sansonia* by its reticulate sculpture and its distinctive peripheral keel. *Microliotia saturnia* (Fig. 15.101B) is the only species known from Australia. *Astrosansonia* is characterised by its planispiral shell. With a diameter of about 1 mm, species of this genus are the smallest Recent representatives of the family. *Astrosansonia dautzenbergi*

(Fig. 15.101F, G) is known from many Indo-Pacific localities, including Christmas Island and Sahul Banks. One of three undescribed Australian species, in a new genus (P. Bouchet personal communication), is illustrated in Figure 15.101C. These species are characterised by a turbinate or rissoiform teleoconch with convex whorls, and the presence of an open umbilicus. One of the species is widespread, and another may be a Western Australian endemic. '*Merelina*' *hians* (Fig. 15.101D) described by Laseron (1956a) and recorded in Australian waters, has very convex whorls, a remarkable clathrate sculpture, and foliate peristome and is probably assignable to another new genus. *Discrevinia* is a monotypic genus, characterised by a pupoid shell, a predominantly spiral sculpture and an axially centred aperture. In Australian waters, *D. balba* (Fig. 15.101E) is known from Christmas Island and Queensland. *Reynellona* is characterised by its aperture forming a narrow forward protruding tube. Though the type species *R. natalis* (Fig. 15.101H; described from Christmas Island by Iredale 1917a) has only axial ribs on its spire, the other species in the genus have two to four nodular spiral cords. Among the latter group are two new species, one collected from Christmas Island and the other from Western Australia. *Chrystella* (Fig. 15.101I) is readily distinguished by its exclusively spiral sculpture. It resembles some rissoids and pyramidellids. *Chrystella islandica* the type species, was described from Christmas Island. *Sherbornia* is a monotypic genus. The specific name of the type species, *S. mirabilis* (Fig. 15.101J, K) recalls its very unusual general appearance, due to the development of an exceedingly large wing-like peristome, together with a multi-tubed aperture. Although the genus has long been classified near the Triforidae, the characters of the protoconch allow a confident allocation in the Pickworthiidae. *Sherbornia mirabilis* was, for many decades, known only from Christmas Island, until shells were collected from Polynesia in the 1970s.

The Pelyciidiidae (Ponder & Hall 1983), are probably closely related to, or even synonymous with, the Pickworthiidae on the basis of new anatomical and radular data (W.F. Ponder personal communication). Although poorly known, the genus *Pelycidion* appears to have a broad tropical distribution in both hemispheres.

Although the family has been traced back to the Eocene in Europe, no fossils are known as yet from Australia.

Superfamily CINGULOPSOIDEA

Cingulopsoidea was created (Ponder 1988a) to include three families of small-sized, mostly conical-shelled, gastropods, the Cingulopsidae, the Eatoniellidae and the Rastodentidae. They share a pegged operculum, an inner organic shell layer and, mostly, a simple conical shell. This superfamily includes some of the smallest molluscs.

The families grouped here were previously included in the Rissooidea (= Truncatelloidea; Cingulopsidae and Rastodentidae) or Littorinoidea (Eatoniellidae). They differ from members of both of those superfamilies in lacking a penis. Cingulopsoideans also differ from rissooideans in having an oesophageal gland, the salivary ducts running through the nerve ring and lacking a crystalline style. They differ from the Littorinoidea in having a discrete organic shell layer on the inner surface of the shell called the 'inner chitinous' layer by Ponder & Yoo (1976), and a pegged operculum. The name, 'inner chitinous' layer, is misleading because the material making up the layer is not chitin (J.D. Taylor personal communication), and it is better referred to as the 'inner organic' layer. Because many of the features of this group are considered to be plesiomorphic (Ponder 1988a), its current classification must be considered tentative. The Barleidae, for example, a member of the Rissooidea, has a pegged operculum and an inner 'organic' shell layer, but is typically rissooidean in other features.

The fossil history of Cingulopsoidea is poorly known, partly because it is very difficult, perhaps impossible, to identify accurately members of these groups on shell characters alone.

Cingulopsoideans are primarily Southern Hemisphere in distribution, although a few reach the northern parts of the Indo-West Pacific and some cingulopsids occur in the Atlantic and Mediterranean.

Family Cingulopsidae

Cingulopsids are marine snails with small pupoid to depressed trochiform shells and a pegged operculum. The radula is taenioglossate, very variable in form and absent in one genus. There are no metapodial or pallial tentacles, and jaws are absent. The oesophagus has two pouches anterior to the nerve ring in some species but is otherwise simple. The stomach lacks a crystalline style and style sac and the intestine is short and simple. Males have no penis, females have a monaulic or diallic reproductive system and a large posterior bursa copulatrix, and the pallial genital ducts in both sexes are closed (Fig. 15.102K, L).

Cingulopsids were included in the Rissoidae until Fretter & Patil (1958) studied the anatomy of the European species, *Cingulopsis* (now *Eatonina*) *fulgida* and as a result proposed the family Cingulopsidae. Ponder (1965b) considerably extended the limits of the family in a study of the New Zealand species and (Ponder 1968a) described the anatomy of a New Zealand species, *Eatonina micans*. Ponder & Yoo (1980) reviewed all cingulopsid genera as well as the Australian and Indo-Pacific species and Ponder (1983b) revised the genera and species found in the Antarctic and Subantarctic. Other family names have been proposed for the group; these include Coriandriidae (Nordsieck 1972) and Eatoniidae (Golikov & Starobogatov 1975).

Shells (Fig. 15.102A–C) are minute (less than 3 mm), pupoid (Fig. 15.102B) to depressed trochiform (Fig. 15.102A), umbilicate to imperforate and smooth or with axial or spiral sculpture. The protoconch is smooth and paucispiral. The aperture is simple and usually lacks a varix. The operculum is paucispiral, oval, transparent, and horny and has a peg arising from the nucleus on the inner surface (Fig. 15.102D–F).

The head-foot is unpigmented or grey or orange to orange-red. The head has a distally bilobed snout and a pair of medium to long cephalic tentacles with the eyes in bulges on their outer bases. The foot (Fig. 15.102J) is simple, long and oval and has an anterior and a posterior pedal gland, the latter with a longitudinal groove reaching to the posterior end of the foot. There are no pallial or metapodial tentacles (Fretter & Patil 1958; Ponder 1965b, 1968a; Ponder & Yoo 1980).

The following anatomical information is from Fretter & Patil (1958) and Ponder (1968a) and supplements information given in the family diagnosis. The ctenidium (Fig. 15.102K) is well developed, with finger-shaped filaments, the osphradium is large and elongate-oval and a well-developed hypobranchial gland is present. The renal organ is simple and opens into the posterior end of the mantle cavity.

Cingulopsids feed on microalgae, diatoms and detritus. The radula (Fig. 15.102G–I) is more variable in tooth shape and cusp pattern than in most neotaenioglossan families. It has small to large central teeth with small to obsolete cusps and, often, basal processes. The lateral teeth are large, variable in shape and cusp pattern. The inner marginal teeth have long prominent cusps. The outer marginal teeth are hook-like or short and triangular. The radula is absent in the genus *Tubbreva*. The stomach is U-shaped and small.

The circumoesophageal ganglia are concentrated, and the supra-oesophageal ganglion lies on the right side, not the left as is usual in neotaenioglossans, indicating that partial euthyneury has taken place (Fretter & Patil 1958).

The European species *Eatonina fulgida* breeds in spring and summer and the eggs are laid singly, on coralline algae, in small, tough, lens-shaped capsules. Development is direct, the young hatching out in the crawling stage (Fretter & Patil 1958).

Cingulopsids are sometimes found in large numbers amongst algae and debris in the lower littoral and sublittoral zones.

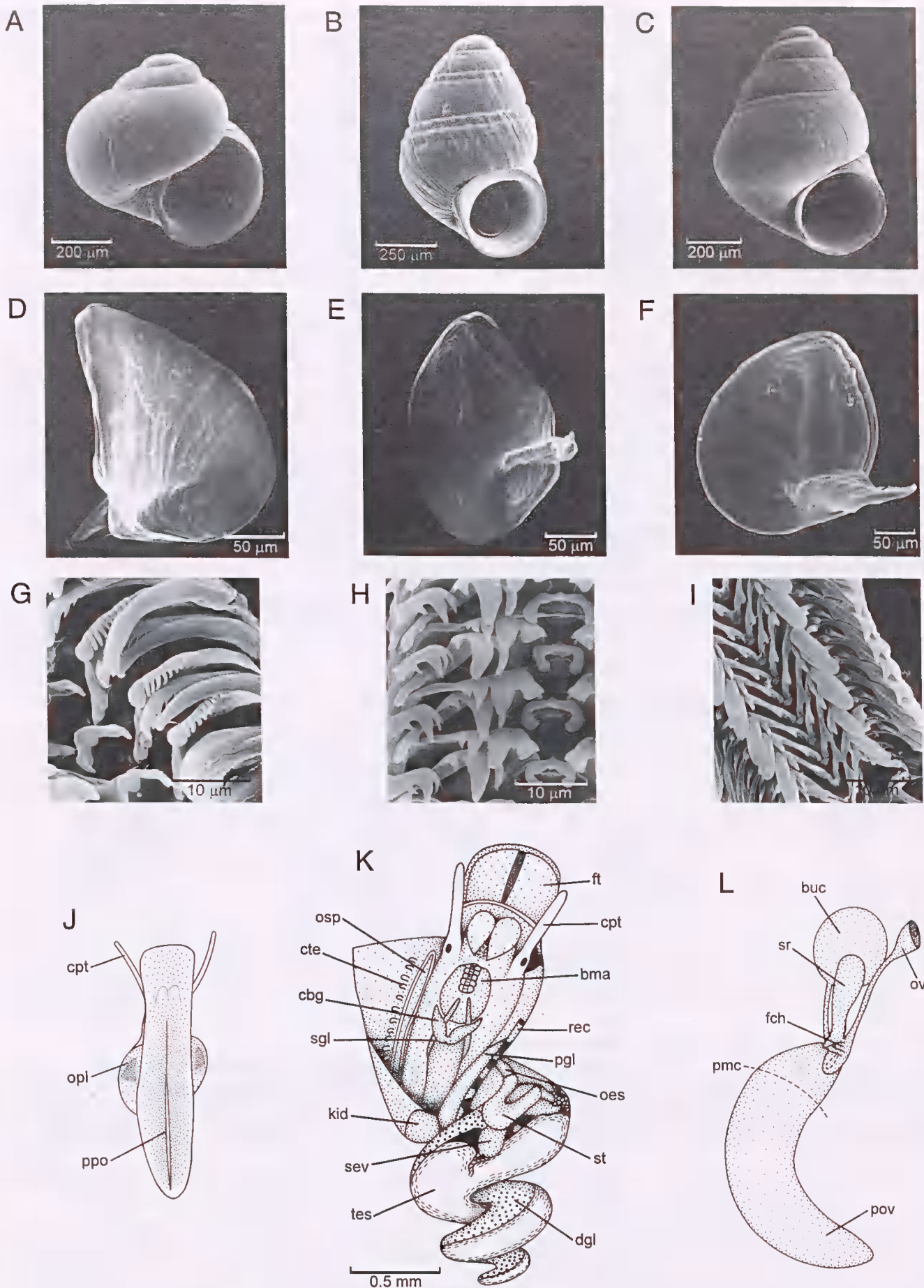


Figure 15.102 Family Cingulopsidae. A–C, shells, apertural view: A, *Skenella (Pilitonia) westralis*; B, *Pseudopisinna gregaria*; C, *Eatonia ardea*. D–F, opercula: D, outer surface and E, inner surface of *Pseudopisinna gregaria*; F, *Eatonia condita*, inner surface. G–I, portions of radulae: G, *Skenella (Pilitonia) westralis*, half transverse rows, showing central, lateral and marginal teeth; H, *Eatonia condita*, half transverse rows, showing central, lateral and marginal teeth; I, *Pseudopisinna costata*, several transverse rows. J, *Eatonia lunulata*, animal, ventral view. K, *Eatonia micans*, male removed from shell and mantle cavity opened dorsally. L, *Eatonia micans*, female genital tract; the dotted line indicates the posterior limit of the mantle cavity. bma, buccal mass; buc, bursa copulatrix; cbg, cerebral ganglion; cpt, cephalic tentacles; cte, ctenidium; dgl, digestive gland; fch, fertilisation chamber; ft, foot; kid, kidney; oes, oesophagus; opl, opercular lobe; osp, osphradium; ov, ovary; pgl, prostate gland; pmc, posterior limit of mantle cavity; pov, pallial oviduct; ppo, opening of posterior pedal gland; rec, rectum; sev, seminal vesicle; sgl, salivary gland; sr, seminal receptacle; st, stomach; tes, testis. (J, after Ponder & Yoo 1980; K, L, after Ponder 1968a) [A–I, W.F. Ponder; J–L, C. Eadie]

15. PROSOBRANCHS

The aperture is simple, ovate to circular, and the outer lip is often strongly excavated. A curved, thickened peg arises from the inner side of the small, marginal nucleus of the paucispiral operculum (Fig. 15.103D, E).

The animal has long, lashing cephalic tentacles, with eyes on swellings at their bases, and a bilobed snout. The opercular lobe may bear one to two short tentacles. There is an anterior pedal gland and a metapodial one that opens into a posterior mucous slit on the sole of the foot. Animals are micrograzers and microdetritus feeders, scraping the diatomaceous film from the substratum. The radula (Fig. 15.103F) has a large, square, central tooth with three to seven cusps and a pair of strong basal processes; the lateral teeth are short and quadrate; the inner marginal teeth are narrow and curved, with a denticulate edge, whereas the outer marginals are curved and finely serrate. The paired jaws are composed of chitinous rods. The salivary glands pass through the circum-oesophageal nerve ring. Large glandular structures open into the posterior end of the buccal cavity, and oesophageal glands are also present (Fig. 15.103G). A style sac is present in the stomach, but there is no crystalline style. In the mantle cavity there is a monopectinate ctenidium, an osphradium and a hypobranchial gland, all well developed. In the concentration of ganglia, the nervous system shows some resemblance to the Cerithioidea.

The males (see Fig. 14.1B) are aphallate, or may bear a rudimentary swelling, and the prostate is open. In females, the pallial oviduct is open; posteriorly a bursa copulatrix and a blind sac open into a muscular diverticulum (Fig. 15.103H). The glands of the pallial oviduct are epithelial. Eggs are large and yolky and fertilisation is internal. No details of reproduction and life history are known, but the form of the eggs and protoconch suggest nonplanktotrophic development.

These are small algal-dwelling molluscs, found mostly in the lower littoral zone, but a few occur on the continental shelf. They can be extremely abundant on intertidal and shallow sublittoral algae in southern Australia and New Zealand, often with several species present in any one locality. They are distributed in the Indo-Pacific, Subantarctic, Antarctic (Ponder 1983b) and South America (Ponder & Worsfold 1994), but reach their greatest diversity in Australasia. The family comprises five genera and about 100 species, of which the two genera *Eatoniella* and *Crassitoniella*, with 20 species, occur in Australia, largely in the south.

A single fossil subspecies is named from the Lower Miocene to Upper Pliocene of Tasmania, Victoria and South Australia (Ponder & Yoo 1978), but others are present. A number of fossil records are known from the Miocene and Pliocene of New Zealand (Beu & Maxwell 1990).

Family Rastodontidae

Rastodontids are minute marine snails with smooth or spirally sculptured conical shells. They have a thick, pegged operculum and are characterised by their highly modified taenioglossate radula.

Ponder (1966a) described two genera, *Rastodens* and *Tridentifera*, and proposed a new family for them, based on the structure of the radula, lack of a ctenidium and absence of a penis. This family (originally Rastodenidae, but later amended to Rastodontidae) contains only a few species from Australia and New Zealand, although the Australian species have not been described. Two species named from Hawaii (Kay 1979) are actually barleeids. The description below is based largely on data on New Zealand taxa, the anatomy of only one species, *Rastodens puerilis*, having been studied (Ponder 1966a).

The shell is minute, solid, conical, smooth or with spiral cords (Fig. 15.104A). The whorls are flat to slightly convex and the aperture is oval to circular. The peristome is not greatly thickened and the outer lip is strongly excavated. The operculum is very like that of eatoniellids, with a strong peg on its inner surface (Fig. 15.104B) which curves from the eccentric nucleus and extends past the columellar edge.

The head has long, prominently ciliated cephalic tentacles which unlike those of members of the other two families in this superfamily have slightly swollen tips (Fig. 15.104D), and prominent, ciliated neck lobes. The foot is long and has an anterior and a posterior pedal gland. The mantle cavity lacks a ctenidium, water circulation being maintained by ciliated ridges bordering the large osphradium, and there is a well-developed hypobranchial gland.

The unusual radula (Fig. 15.104C) has large central teeth with three to seven long spike-like cusps (the central one largest), sometimes with intermediate spikes, and is somewhat reminiscent of some rachiglossate radulae. The lateral teeth are elongate and each has one to several long, spike-like cusps. The inner marginal teeth have thick, broad bases and an elongate cusp sometimes subdivided into two to three subsidiary cusps. Outer marginal teeth are long, straight, wide or narrow basally, the terminal portion being very narrow and the tip blunt or with two very small cusps. Rastodontids are found associated with bryozoans and hydroids and they are presumed to feed on these animals, perhaps on individual polyps or zooids.

The pallial genital tracts are closed and there is no penis, but details of the internal anatomy are sketchy. Like other members of the superfamily, rastodontids lack a crystalline style in the stomach and have an oesophageal gland.

Nothing is known about rastodontid life histories, but the protoconch morphology suggests that development is direct. No fossils have been recognised as members of this family.

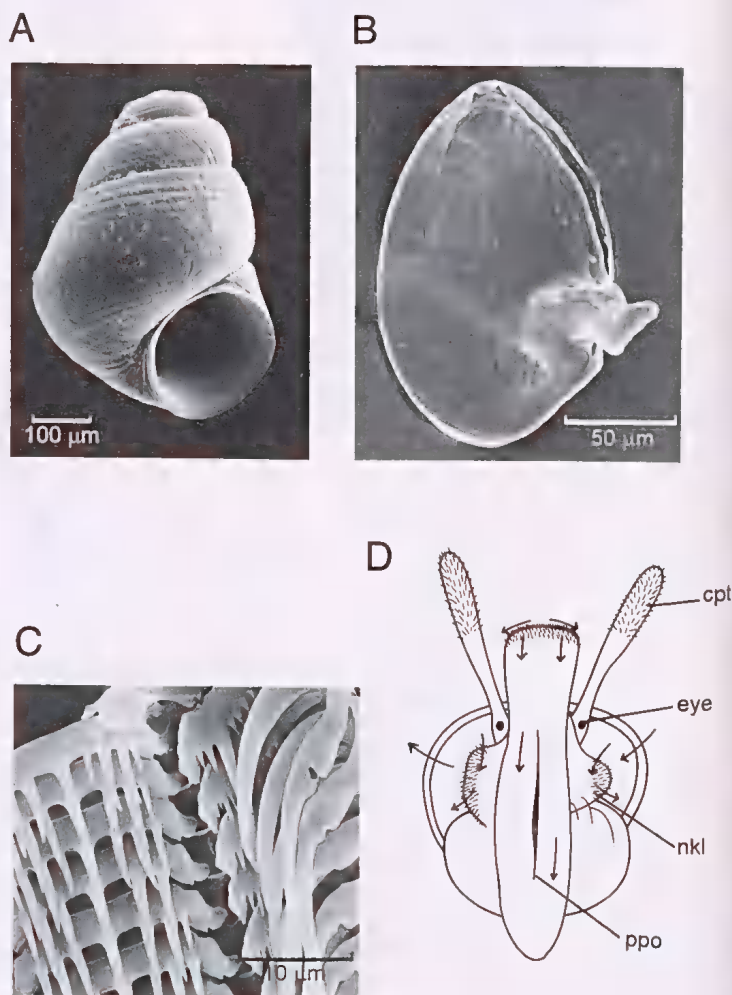


Figure 15.104 Family Rastodontidae. A–C, *Rastodens* sp.: A, shell, apertural view; B, operculum, inner surface; C, half rows of radula, showing the long spike-like cusps on the central tooth. D, *Rastodens puerilis*, animal, ventral view, with arrows indicating water currents and the direction of ciliary currents. cpt, cephalic tentacle; eye, eye; nkl, neck lobe; ppo, opening of posterior pedal gland. (D, after Ponder 1966)

[A–C, W.F. Ponder; D, C. Eadie]

Superfamily Rissooidea

The Rissooidea (= Truncatelloidea) is the largest, most diverse neotaenioglossan superfamily and one of the largest gastropod groups. Rissooideans are generally poorly known because of their small size and often simple, rather featureless shells. They have not only evolved to occupy almost all aquatic habitats, but some are amphibious, living in marginal areas such as swamps, salt marsh and mangroves and there are also fully terrestrial groups. Some aspects of the evolution and relationships of the superfamily have been reviewed recently (Ponder 1988a) and the classification adopted in that paper is utilised here.

The superfamily has no known autapomorphies, is possibly paraphyletic or even polyphyletic, and can only be diagnosed on a combination of character states. Members are small-sized, phallate neotaenioglossans lacking a siphonate aperture, without a well-developed oesophageal gland, with a crystalline style and with the salivary glands not passing through the nerve ring. They appear to be most closely related to the Littorinoidea and Cingulopsoidea, but differ from both of those groups in the salivary gland and oesophageal characters noted above. Cingulopsoideans lack a penis, but in common with some rissooideans, the Barleeidae and some Anabathridae, have an inner organic shell layer, a pegged operculum and a long posterior pedal gland opening (Ponder 1988a). These three features are probably plesiomorphic in Rissooidea.

Rissooideans are small-sized (rarely greater than 10 mm in length) and include some of the smallest molluscs. They exhibit a large diversity of shell types ranging from planispiral to very elongate, and from tightly to loosely coiled or even uncoiled and tusk-like. No limpet-like forms are known. The aperture is circular to ovate, with or without shallow channels anteriorly and posteriorly, but never producing a true anterior canal. Sculpture and periostracal development vary considerably within the group. An operculum is present which may be circular or ovate, with the nucleus central, eccentric or submarginal and is composed of horny material, sometimes with white (sometimes calcareous) deposits. The inner opercular surface is either smooth or bears one or more pegs and/or ridges.

The cephalic tentacles are paddle-shaped, strap-like or tapering, often with tracts of active cilia, sometimes with cilia on the proximal part of the left tentacle more strongly developed than on the right. There are paired or single pallial tentacles present in some groups and some have a metapodial tentacle (divided into three in *Alvania*) on the dorsal part of the foot behind the operculum. Tentacles are never developed on the opercular lobes or on the sides of the foot. An anterior pedal gland is always present, opening beneath the propodial flap into a horizontal groove across the anterior edge of the foot. A posterior pedal gland is present in some families and opens into the middle of the metapodium by way of a short aperture which may be located in a short to long groove. The latter configuration is thought to be the plesiomorphic state (Ponder 1988a), with the groove extending to the posterior end of the foot (in Barleeidae, Anabathridae and Emblandidae), a condition also typical of the Cingulopsoidea.

The mantle cavity typically contains a ctenidium with triangular to finger-shaped filaments, a short to long oval osphradium; a hypobranchial gland is usually present. The rectum and pallial genital duct lie in the right pallial wall.

Most of these animals have a microphagous diet, although some ingest decaying vegetation. Most scrape bacteria, diatoms, etc., from the surface of algae (Fretter & Graham 1962, 1978; Fretter & Manly 1979) or other substrata such as sand grains (Lopez & Kofoed 1980), and a few rissoids and *Emblanda* feed on foraminiferans (Ponder 1985a, 1985c). The digestive system is only slightly modified. There is usually a pair of jaws and a typical taenioglossate radula is present in nearly all taxa although this has been modified in the Emblandidae (Ponder 1985c) with the loss of two tooth rows. The simple, tubular salivary glands do not pass through the nerve ring, a condition atypical of most other neotaenioglossans and an autapomorphy of the superfamily,

although one species is known to sometimes have the salivary glands passing through the nerve ring (Bieler & Mikkelsen 1988). The mid-oesophagus has well-developed dorsal folds, but does not have an oesophageal gland, although vestiges of this structure are found in some taxa. The large stomach has a short crystalline style and the intestine and rectum are simple. The rectum is usually straight, rarely forming one or two loops on the pallial roof.

The renopericardial system consists of a monotocardian heart and a large kidney which abut one another and typically lie immediately behind the posterior pallial wall with the renal opening on that wall. In some taxa, the kidney (and sometimes the pericardium) bulge into the roof of the mantle cavity, especially in *Bithynia* (Fretter & Graham 1962). A well-developed renal gland is usually present on the outer renal wall. Often in females a gono-pericardial canal is present and rarely there is a duct between the kidney and the renal part of the oviduct.

Most rissooideans are dioecious, but one vitrinellid species (*Cyclostremiscus beaulti*; Bieler & Mikkelsen 1988) has been shown to be a protandrous hermaphrodite. It is possible that this phenomenon may be more common in the superfamily than is presently recognised, although other vitrinellids investigated are dioecious (Ponder 1994b). Females with non-functional penes are not uncommon in some species of Rissoidae (Thiriou-Quiévreux 1977; Ponder 1985a), but hermaphroditism has not yet been demonstrated in that family and this phenomenon is probably due to pseudohermaphroditism or imposex (Fioroni, Oehlmann & Stroben 1991). One hydrobiid, *Potamopyrgus antipodarum*, is known to be parthenogenetic (Boycott 1919).

The testis is composed of lobule-like acini, and is situated on the posterior side of the digestive gland. It usually extends from the posterior part of the stomach, often almost to the posterior end of the visceral coil. The vas deferens is usually expanded and coiled, forming a seminal vesicle which lies behind the anterior part of the stomach, sometimes beneath the testis, although it is often narrow and more or less straight as it passes over the anterior gastric chamber and opens to the prostate gland at the posterior end of the mantle cavity. The prostate gland may bulge back into the kidney or lie entirely in the right pallial wall. It is primitively an open glandular groove, but is more usually closed or partially closed. The pallial vas deferens is normally closed, rarely an open groove, and runs to the base of the penis near which it sometimes thickens and develops muscular walls, forming an ejaculatory duct. The penis may or may not have accessory lobes and/or glands, and is situated behind the right eye in most families, although centred in Anabathridae. The penial duct shows all gradations from a primitive external groove to an internal muscular duct.

In females, the ovary lies in the same position as the testis of the male, but it is usually shorter. The upper oviduct is a very thin-walled tube which thickens as it passes by the kidney (the renal part of the oviduct) and sometimes receives a duct from the pericardium or, rarely, the kidney. The renal oviduct is sometimes glandular (as in Rissoidae and Emblandidae) and may be coiled (as in Hydrobiidae, Pomatiopsidae and Anabathridae). One or more simple sac-like seminal receptacles open to the renal oviduct in most taxa. The renal oviduct opens to the posterior part of the oviduct gland, which usually functions as an albumen gland, the anterior part being the capsule gland. The pallial part of the glandular oviduct lies in the right pallial wall and is usually closed (open ventrally in a few genera in several families), with a sperm channel ventrally. In some groups, the sperm channel has been separated from the oviduct glands to form a separate tube which independently opens anteriorly or posteriorly in the mantle cavity. This diallic arrangement has been acquired convergently in several families (Ponder 1988a). There are many modifications, novel arrangements and convergences in the female reproductive system, sometimes through linkages with the renopericardial system (see Ponder 1988a for an overview). Eggs are usually laid in hemispherical capsules, however details are not known for many groups. Planktonic larval development occurs in several families but direct development is typical of the freshwater and terrestrial taxa.

15. PROSOBRANCHS

The nervous system is of the typical neotaenioglossan form, and the circumoesophageal ganglia vary in degree of concentration. Detailed studies on the nervous system are few, by far the most comprehensive being those by Davis (1967) on two species of Pomatiopsidae. The cerebral ganglia lie close together or abut one another and the corresponding pleural and cerebral ganglia usually abut or fuse. The suboesophageal ganglion typically has a short connective with the left pleural ganglion and the supra-oesophageal ganglion has a short to long connective with the right pleural ganglion. The pedal ganglia are connected by a short commissure or abut one another. Two pairs of cords, each bearing a single ganglion, emerge from the antero-ventral and ventral edges of the pedal ganglia. The upper pair of ganglia are the propodial ganglia and the lower pair the metapodial ganglia. There are no commissures between these ganglia. A pair of statocysts lie against the posterior edge of the pedal ganglia and contain a single statolith. In males, the penial nerve arises from either the dorsal surface of the right pedal ganglion or the right pleuropedal connective (most families), rarely from the right pleural ganglion (Bithyniidae) or from the right cerebral ganglion (Anabathridae, Emblandidae) (Ponder 1988a). The eyes, located in bulges at the outer bases of the tentacles, are sometimes reduced to a rudiment as seen in some taxa living in the deep sea or in subterranean waters. The osphradium is well developed, but simple, in almost all rissooideans and is encircled with a ciliated ridge which sometimes provides the respiratory current when the ctenidium is very reduced or lost.

Rissooideans are found in all oceans and in fresh and brackish waters virtually worldwide. True terrestrial groups (some truncatellids and assimineids) are much more restricted in their distributions, occurring in some tropical and subtropical areas. The earliest undoubted Rissooidea are found in Middle Jurassic rocks (Ponder 1988a), but the group probably arose much earlier.

Early work on members of this superfamily, as with so many other shelled molluscs, concentrated on shell morphology. Because the shells of many rissooideans are simple and frequently rather similar in appearance, often due to convergence, their homoplasious nature is only recognised following anatomical studies. For example, numerous studies on the two major freshwater groups, Hydrobiidae and Pomatiopsidae, have shown that shell and even radular morphology are not reliable guides to relationships and the classification of these groups is now largely based on internal anatomy (see references under those families). Most families are still poorly known and a great deal of work remains to be done. The rather large marine 'family' Vitrinellidae is so poorly studied that only a very few species have been investigated anatomically and even some family-group taxa are still unknown anatomically (for example Epigridae, Ctiloceratinae). Further comparative anatomical studies will undoubtedly alter the present arrangement of family-level groupings.

Some authors (for example, Golikov & Starobogatov 1975) have split this superfamily into several smaller groups, but there is little justification for this on available evidence. Ponder (1988a) pointed out that there were two main groups within the Rissooidea (as Truncatelloidea) based primarily on the histology of the oviduct glands, although a few apparently intermediate taxa exist (for example Caecidae).

There has been disagreement as to the name of the superfamily, the name Truncatelloidea having priority, but a recent International Commission of Zoological Nomenclature ruling (ICZN Opinion 1664) has given precedence to the long-used Rissooidea (Rosenberg & Davis 1990).

The family-level classification of this group is also the subject of some debate, the classification adopted here being a relatively conservative one. Some families, as recognised here, have been split into many different family groups by some workers. For example, Ponder & Warén (1988) listed 46 family-group names that they include within the Hydrobiidae and 12 in the Rissoidae.

Many of the freshwater species tend to speciate readily because of their poor powers of dispersal and are thus potentially ideal subjects for evolutionary studies (for example, Davis 1979; Ponder, Clark, Miller & Toluzzi 1993; Ponder, Colgan, Clark, Miller & Terzis 1994). In addition, many species have very restricted distributions and thus their continued survival is often under threat from human activities. This is particularly true for Hydrobiidae in Australia and elsewhere (Ponder 1994c; see also Chapter 1).

Rissooideans have little direct economic value. They may play an important part in the food chain either as adults or as larvae (for example, Lebour 1934). Many species also harbour intermediate stages of parasites that infect vertebrates, including humans. The most important among these are some pomatiopsids that are the intermediates host of human blood flukes (*Schistosoma*) (Davis 1980). The New Zealand parthenogenetic hydrobiid, *Potamopyrgus*, has spread rapidly through Europe and south-eastern Australia and Tasmania (Ponder 1988c) and has such a high reproductive rate that it can be a nuisance in water supply systems, as well as possibly displacing native species.

Family Barleeidae

Barleeids are marine snails with small to minute (less than 5 mm in length) shells characterised by a protoconch sculptured with pits, an organic inner shell layer and a convex, thickened, one-layered operculum (Fig. 15.105B, C) that has a prominent peg and a longitudinal ridge on the middle part of the inner surface.

Barleeids were included previously in the Rissoidae, but have been given family status (Ponder 1983a) on the basis of anatomical and other morphological differences. Originally, they were combined with the Anabathridae, but this group has since (Ponder 1988a) been separated from the Barleeidae. The shells are solid, broadly ovate to conically elongate and with or without a narrow umbilicus. An inner organic shell layer is present and is moderately to poorly developed. The teleoconch surface is smooth or has axial or spiral sculpture or both. The aperture is angled posteriorly, angled to convex anteriorly, with a simple peristome and a prosocline to opisthocline outer lip which has a varix in some taxa. The dome-shaped protoconch is sculptured with minute pits.

The two genera that occur in Australia differ in their shell sculpture. Species of *Barleeia* have smooth or weakly spirally sculptured shells without spiral ridges on the protoconch, and have a red operculum (Fig. 15.105A). Species of *Protobarleeia* have spirals on the protoconch and teleoconch, and have a yellow operculum.

The foot is usually short and broad and typically has a longitudinal slit on the sole that reaches to the posterior end, into which the posterior pedal gland opens (Fig. 15.105F). The ctenidium has well-developed, finger-shaped filaments and the osphradium is about half its length and elongate-oval.

Barleeids are detritus-feeders (Graham 1955; Fretter & Graham 1962). The central teeth of the radula (Fig. 15.105D, E) have triangular cutting edges. These and lateral teeth have few cusps, and the marginal teeth have several small cusps on their outer edges. Oesophageal pouches are present in *Barleeia* (the anatomy of *Protobarleeia* is unknown). The kidney is simple and sac-like, with a renal gland on the outer wall.

The penis is large, usually simple, and is situated behind the right eye. The female pallial duct varies in detail between genera, some having a posterior bursa copulatrix with an opening separate from the distal oviduct opening, others (as in *Barleeia*) having a common distal opening for copulation and egg laying. Species of *Barleeia* lack a bursa copulatrix; instead they store sperm in a modified area of the albumen gland. They are diaulic, having a posterior sperm duct opening to the mantle cavity (Ponder 1983a). The reproductive biology and the life cycle of the European species, *Barleeia unifasciata*, were investigated by Southgate (1982), who found that this species lives for a maximum of two years.

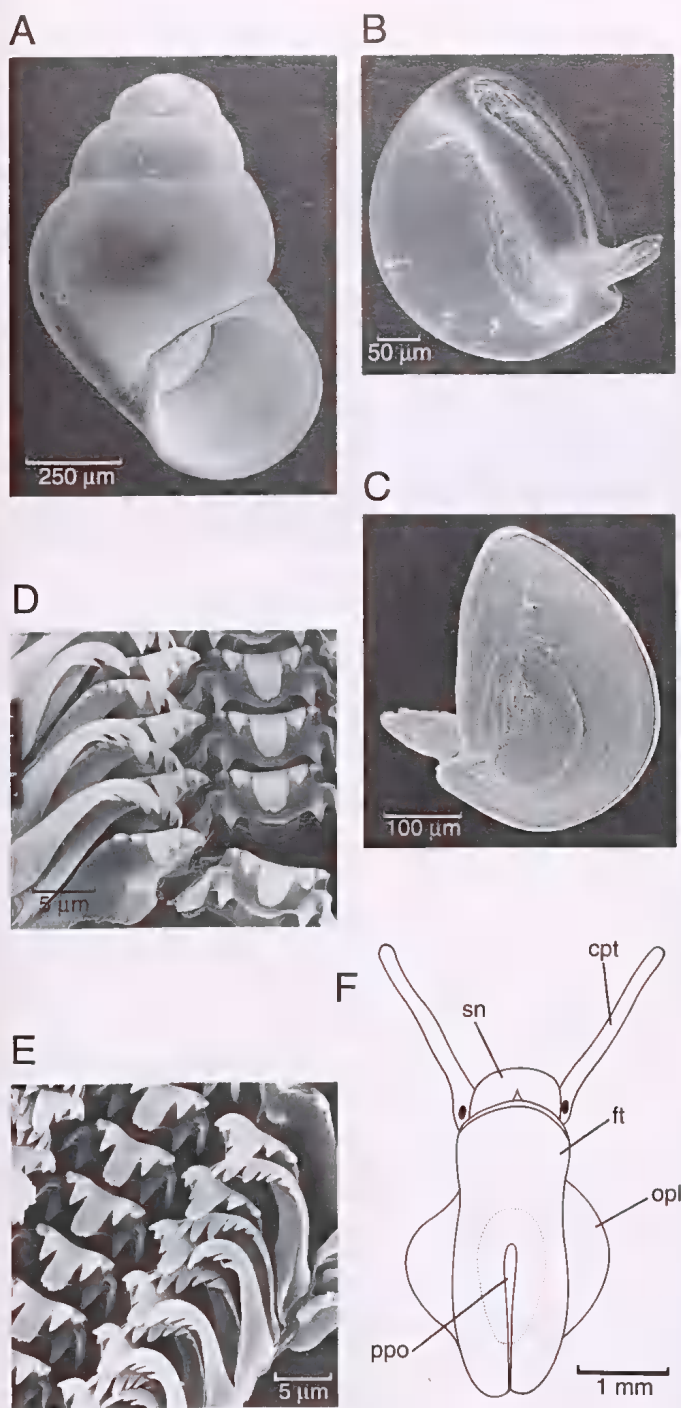


Figure 15.105 Family Barleeidae. A–D, *Barleeia* sp., a new species from Point Quobba, Western Australia: A, shell, apertural view; B, operculum, inner surface; C, operculum, outer surface; D, teeth on one side of radula. E, *Protobarleeia myersi*, teeth on one side of radula. F, *Barleeia unifasciata*, head-foot, ventral view. cpt, cephalic tentacle; ft, foot; opl, opercular lobe; ppo, posterior pedal gland opening; sn, snout. (F, after Ponder 1983a) [A–E, W.F. Ponder; F, C. Eadie]

Barleeid fossils are not known before the Eocene, but the group is presumed to be Mesozoic in origin (Ponder 1988a). Fossil barleeids are not common, probably due to the preference of barleeids for rocky shallow-water habitats. *Protobarleeia* is known from the Upper Miocene of Eniwetok Atoll (Ladd 1966).

Family Anabathridae

These minute marine snails resemble barleeids in their size and in having a pitted protoconch microsculpture, and an inner organic shell layer, but differ in having a flat operculum composed of two layers, usually without a peg (a short peg is rarely present) and lacking a longitudinal ridge on the middle part of the inner surface. They differ from all other rissoidaeans, except Emblandidae, in having the penis innervated by the cerebral ganglia (Ponder 1988a) instead of a pedal innervation.

Previously, along with the Barleeidae, members of this group were included in the Rissoidae. More recently they were considered to be a subfamily of the Barleeidae (Ponder 1983a), but are now given family status (Ponder 1988a).

Shells are solid, elongately pupoid to broadly ovate, and with or without an umbilicus (Fig. 15.106A–D). The inner organic layer (Ponder & Yoo 1976) of the shell is well developed. The aperture is usually not channelled and has a simple or duplicated peristome. A varix is usually present on the outer lip (except in *Badepigrus* and *Pseudestrea*) and the outer lip is prosocline to opisthocline. The teleoconch is smooth or has axial or spiral sculpture. The protoconch has minute pits arranged in spiral rows, and is dome-shaped and paucispiral (Fig. 15.106H). The two layered, flat operculum is diagnostic (see above) and may have a ridge along the inner (columellar) edge (Fig. 15.106F).

The foot is short, with an anterior pedal gland and sometimes a posterior pedal gland with a long slit as in the Barleeidae (Fig. 15.106I). The osphradium is elongate-oval and a little shorter than the ctenidium. Anabathrids are microphagous feeders that lack an oesophageal gland, although the mid-oesophagus bears a pair of long dorsal folds. The radula (Fig. 15.106G, H) is taenioglossate and differs significantly between the genera (Ponder 1983a). The kidney differs from the Barleeidae and most other rissoidaeans, in lacking an obvious renal gland on the outside wall.

The penis differs from the simple, straight structure seen in the Barleeidae, in being coiled and situated at about the midline of the head just behind the eyes (Fig. 15.106J). The female has a posteriorly placed bursa copulatrix and is either diaulic or monaulic (Fig. 15.106K, L). Development is assumed to be direct (Ponder 1983a), but nothing is known of anabathrid reproductive biology.

Many of the species in this family are abundant in intertidal and shallow sublittoral areas, particularly in temperate Australia, living on algae and beneath rocks and stones. Some species are found on the continental shelf and a few on the continental slope.

In the most recent generic revision of this family, Ponder (1983a) recognised eight genera, six of which occur in Australia (*Anabathron*, *Amphithalamus*, *Microdryas*, *Badepigrus*, *Pisinna*) and *Pseudestrea*. The genus *Pisinna*, with about 60 taxa in Australia, appears to have its centre of speciation in New Zealand and temperate Australia. A few species are also found in the tropical Indo-West Pacific and one (the type species) in the Mediterranean. *Amphithalamus* and *Anabathron* are also speciose genera, the former having eastern Pacific and Caribbean species, whereas *Anabathron* is restricted to Australia. Of the other three genera, *Microdryas* is also known from New Zealand and South Africa, *Pseudestrea* also from New Zealand, and *Badepigrus* is known only from Australia.

Species of *Pisinna* first appear in the Middle Oligocene of New Zealand, and in the Lower Miocene of southern Australia. As the fossil record is poor for shallow-water, hard-shore environments, this should not be taken as a definitive indication of the age of the group. The taxonomy of the fossil species of the other genera is

Barleeids are found mainly in shallow marine habitats. Little is known about their ecology, but they are often numerous on algae in the sublittoral and lower littoral zones in temperate and subtropical areas, especially in the eastern Atlantic and Mediterranean and on the west coast of North America.

This family comprises five genera (Ponder 1983a), two of which are known to occur in Australia. The genus *Barleeia* has a worldwide distribution, but *Protobarleeia* is known only from the western Pacific Ocean. The greatest diversity of species is found on the west coast of North and Central America, in West Africa and islands in the eastern Atlantic (Gofas 1995). There are at least three undescribed species of *Barleeia* known from Australia (W.F. Ponder personal observation). *Protobarleeia myersi* has been found in Queensland (Ponder 1983a).

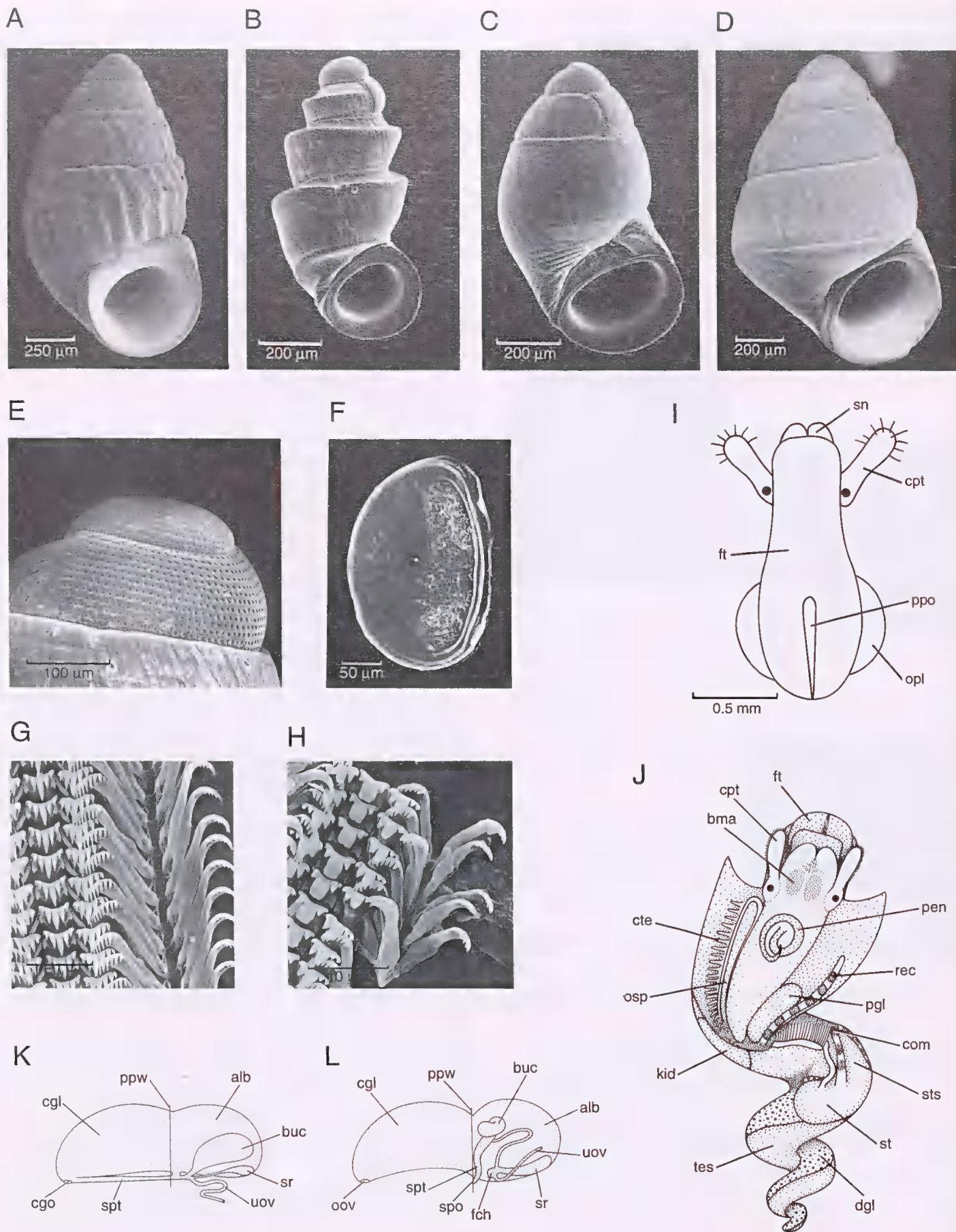


Figure 15.106 Family Anabathridae. A–D, shells, apertural view: A, *Pisinna olivacea*; B, *Anabathron (Anabathron) contabulatum*; C, *Anabathron (Scrobs) luteofuscus*; D, *Amphithalamus (Amphithalamus) incidatus*. E, protoconch of *Amphithalamus (Amphithalamus) incidatus*. F, *Anabathron (Scrobs) luteofuscus*, inner surface of operculum. G, H, portions of radulae showing the central, lateral and marginal teeth on one side: G, *Anabathron (Scrobs) luteofuscus*; H, *Pisinna tropica*. I, *Anabathron contabulatum*, head-foot, ventral view. J, *Pisinna zosterophila*, a male removed from its shell, with the mantle cavity opened. K, L, female genital systems as seen from the left (inner) side: K, *Badepigures pupoides*; L, *Pisinna olivacea*. alb, albumen gland; bma, buccal mass; buc, bursa copulatrix; cgl, capsule gland; ego, common genital opening; com, columellar muscle; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; fch, fertilisation chamber; ft, foot; kid, kidney; oov, oviducal opening; opl, opercular lobe; osp, osphradium; pen, penis; pgl, prostate gland; ppo, posterior pedal gland opening; ppw, position of posterior pallial wall; rec, rectum; sn, snout; spo, spermathecal opening; spt, spermathecal tube; sr, seminal receptacle; st, stomach; sts, style sac; tes, testis; uov, upper oviduct. (I, K, L, after Ponder 1983; J, after Ponder 1968)

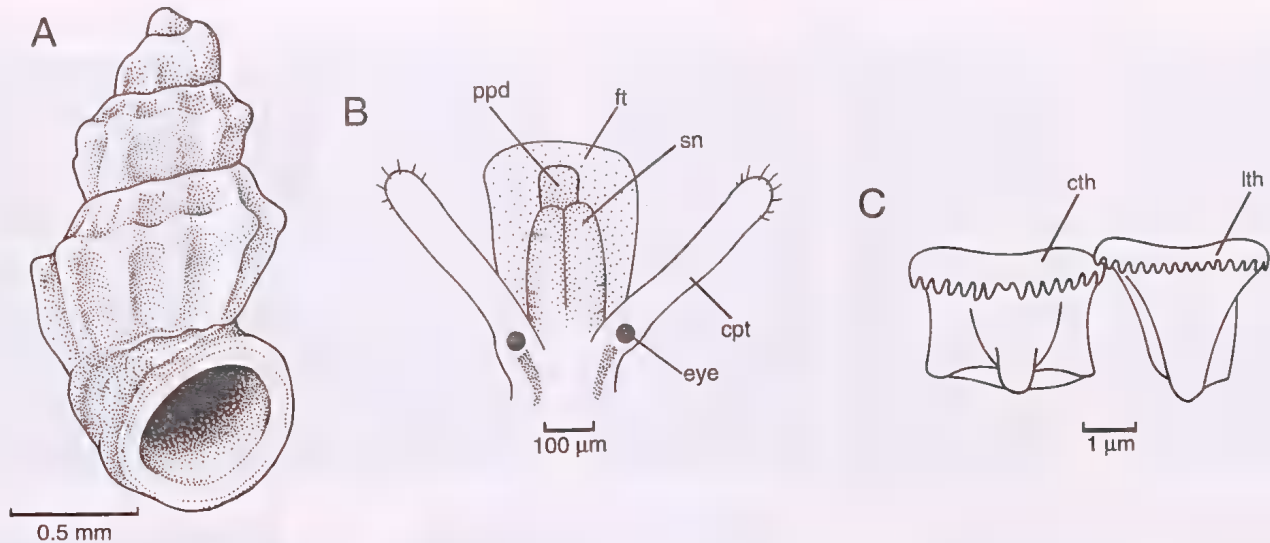


Figure 15.107 Family Emblandidae. *Emblanda emblematica*: A, shell, apertural view; B, head-foot, dorsal view; C, details of the central tooth and one of the lateral teeth, two of the three teeth of each radular row. cpt, cephalic tentacle; cth, central tooth; eye, eye; ft, foot; lth, lateral tooth; ppd, propodium; sn, snout. (B, C, after Ponder 1985b) [A, S. Weidland; B, C, C. Eadie]

not sufficiently well known to give any account of their stratigraphic range in Australia. Ponder (1965c) reviewed the New Zealand Recent and fossil species, and (1968) described the anatomy of a New Zealand species of *Pisinna*.

Family Emblandidae

This monotypic family is based on a minute marine snail, *Emblanda emblematica*, which reaches about 2 mm in shell length. The shell is solid and non-umbilicate, with axial and spiral ribs. The radula is triseriate, jaws are absent and the cephalic-innervated penis is housed in a sheath in the hypobranchial gland. The general morphology of *Emblanda* seems to suggest that it shares a common ancestry with anabathrids (Ponder 1988a).

Emblanda emblematica, a south-eastern Australian endemic, was included in the Rissoidae until Ponder (1985c) placed it in its own family because of major differences, in the radula and anatomy, from other members of the Rissoidae. The description below is based on the information provided in that paper.

The shell (Fig. 15.107A) is ovate-conic with a paucispiral, dome-shaped protoconch which is minutely and irregularly pitted. The aperture is subcircular with an entire, duplicated peristome which lacks distinct notches and has a varix on the outer lip. The operculum is oval, thin, composed of two layers and has an eccentric nucleus. The foot is simple with only an anterior pedal gland, which opens beneath the narrow propodium (Fig. 15.107B). There are no pallial tentacles, but a rudimentary metapodial tentacle is present. A large osphradium occupies the left side of the mantle cavity, which also contains a much reduced gill and a thick hypobranchial gland.

The alimentary canal differs from that of other members of the superfamily in having a very small triseriate radula (Fig. 15.107C). The digestive gland duct also differs in being long and narrow. *Emblanda emblematica* apparently feeds on foraminiferans, these being found in the stomach of dissected specimens. Some features of the alimentary canal that are shared with the rissoid *Rissoina chathamensis* (see Ponder 1968a), which also feeds on foraminiferans, include a long posterior stomach chamber and a very short style sac.

The penis is situated behind the right eye and is enclosed in a sheath behind the hypobranchial gland. The female, in common with those of Rissoidae, has a coiled upper glandular oviduct which probably opens to the albumen gland. Direct development is inferred from the paucispiral protoconch.

Emblanda emblematica lives amongst algae in the lowest littoral and shallow sublittoral zones in New South Wales and Victoria. Although empty shells of *E. emblematica* are not uncommon, living specimens are rarely collected. There is no known fossil history.

Family Rissoidae

The Rissoidae are a family of minute to small (1–15 mm in length) marine to brackish-water snails with ovate to elongate-conical, thin to solid shells. They do not have an inner organic shell layer and the operculum is one layered, thin to thick, with an eccentric nucleus and with or without a peg on its inner surface. The 'renal' oviduct is modified to form a gland (the upper oviduct gland) which lies posterior to the bursa copulatrix.

Rissoids are very diverse and are difficult to classify because of convergence in shell form of different genera. The taxonomic reviews of Wenz (1938–1944), Coan (1964) and Nordsieck (1972) relied on shell characters to classify this large and diverse group which served as a 'dumping ground' for many small-sized gastropods with rather simple shells. Ponder, in 1967, used anatomical characters of mostly New Zealand species as the main basis for a new classification and subsequently (Ponder 1985a), further refined the group and reviewed the world genera using a combination of characters of the shell, radula, head-foot and internal anatomy. Two subfamilies (recognised as families by some previous workers) are recognised, Rissoinae and Rissoininae.

The protoconch has from about one and a half to several whorls, and is smooth or sculptured with spiral, zigzag, reticulate or dotted patterns (Fig. 15.108F, G); it never has predominantly axial sculpture. Teleoconch sculpture, when present, may be reticulate, axial or spiral (Fig. 15.108A–E). Teleoconch whorls are flat to moderately convex, rounded to strongly angled and the umbilicus is usually small or closed. The peristome is simple or duplicated and the outer lip has an external varix in some taxa. The aperture may have a weak sinus posteriorly and may or may not have a channel anteriorly. The columella is usually slightly concave or straight. The operculum is oval to subcircular, horny and paucispiral. If the operculum is thin then there is usually no peg (an exception being the common Australian and Indo-West Pacific genus *Lucidestea*; Fig. 15.108H), but there is a stout peg on the thick operculum of species of *Rissoina*.

Rissoids like most other rissoidaeans, crawl by the action of pedal cilia in a mucous film. The foot always has an anterior pedal gland and, in some species, there is a posterior pedal gland which has a small pore or short slit-like opening (Fig. 15.108N). Metapodial and pallial tentacles are sometimes present.

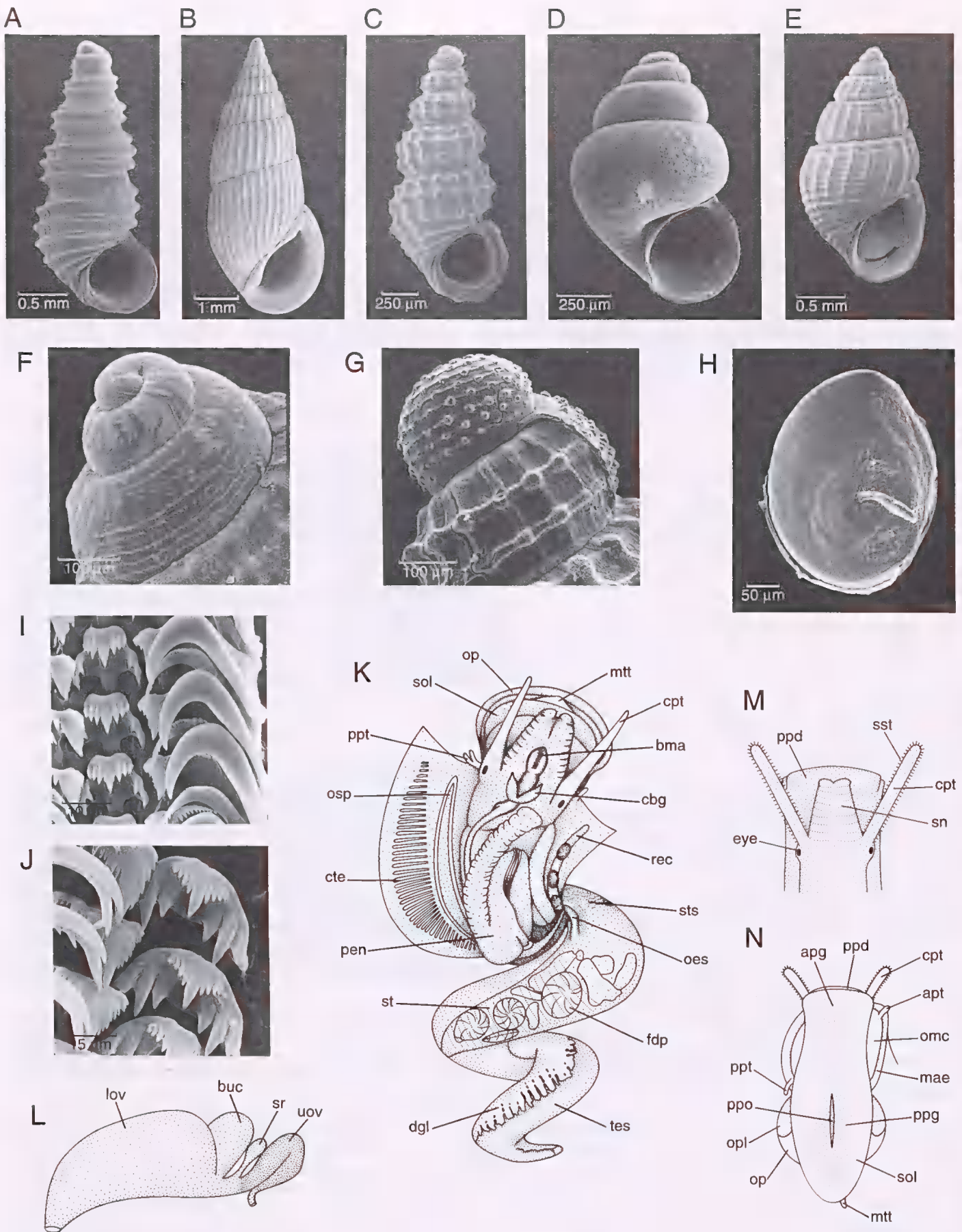


Figure 15.108 Family Rissoidae. A–E, shells, apertural view: A, *Lironoba australis*; B, *Rissoina pulchella*; C, *Merelina elegans*; D, *Lucidestea atkinsoni*; E, *Alvania novanensis*. F, G, protoconchs: F, *Alvania novanensis*; G, *Merelina queenslandica*. H, *Lucidestea atkinsoni*, inner surface of operculum. I, J, radulae: I, *Pusillina (Haurakia) marmorata*, teeth on one side of radula; J, *Lucidestea atkinsoni*, teeth on one side of radula showing details of central teeth. K, *Rissoina chathamensis*, a male removed from its shell, the mantle cavity opened. L, *Onoba* sp., generalised female reproductive system. M, head-foot of a generalised rissoid, ventral view. apg, anterior pedal gland; apt, anterior (left) pallial tentacle; bma, buccal mass; buc, bursa copulatrix; cbg, cerebral ganglion; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; eye, eye; fdp, food particles; lov, lower oviduct gland; mae, mantle edge; mtt, metapodial tentacle; oes, oesophagus; omc, aperture and opening to mantle cavity; op, operculum; opl, opercular lobe; osp, osphradium; pen, penis; pgl, prostate gland; ppd, propodium; ppg, posterior pedal gland; ppo, posterior pedal gland opening; ppt, posterior pallial tentacle; rec, rectum; sn, snout; sol, sole of foot; sr, seminal receptacle; st, stomach; sts, style sac; tes, testis; uov, upper oviduct gland. (K, after Ponder 1968; L, after Ponder 1985a; M, N, after Ponder 1984a)

[A–J, W.F. Ponder; K–N, C. Eadie]

The mantle cavity has a well-developed osphradium which is nearly as long as the well-developed ctenidium; the latter is rarely absent. The kidney is simple and has a well-developed renal gland.

Most of the species that live on macroalgae probably feed on the diatomaceous film covering these algae. Some species that live in other habitats feed on foraminiferans, but usually also have other food items in their stomachs. Some are selective deposit-feeders, and may feed on organisms such as diatoms, dinoflagellates and other unicellular 'algae'.

The jaws are small and composed of simple rodlets. The radula (Fig. 15.108I, J) has small to moderate, triangular to rectangular, central teeth, each with several cusps. The lateral teeth are elongate and have several cusps on each side of the primary cusp. The marginal teeth are also elongate and sickle-shaped with small cusps. There is no oesophageal gland and in this and other respects the alimentary canal resembles that of most other rissoideans.

Males have simple (most Rissoinae) or complex (most Rissoininae) penes situated behind the right eye (Fig. 15.108K); the pallial part of the prostate gland is usually closed or partially closed, rarely open. Females are monaulic and the renal oviduct is modified to form a posterior oviduct gland (Fig. 15.108L) which sometimes has associated multiple seminal receptacles. Rissoids have planktotrophic larvae or undergo direct development. Some genera, such as *Alvania* and *Rissoina*, contain many species with planktotrophic larvae. These genera are distributed worldwide, or throughout the Indo-West Pacific region (for example, *Lucidestea*). Others, such as the Australasian genera *Attenuata* and *Lironoba*, species of which probably undergo direct development, are restricted in distribution. There are, however, exceptions to this generality. For example, nearly all species in the worldwide genus *Onoba* appear to have direct development, and *Rissoa*, with most species having planktotrophic development, is restricted to the eastern Atlantic and Mediterranean Sea.

Almost all information concerning eggs and larvae has been obtained from European species (Lebour 1934; Fretter & Graham 1962). Egg capsules, laid on rocks, algae, sea grasses and other substrata, vary from lens-shaped to spherical and contain from one to 100 eggs. The egg capsules of species with free-swimming veliger larvae tend to contain smaller and more numerous eggs than those of species with direct larval development. The European *Alvania* and *Rissoa* species have egg capsules which contain from six to 100 eggs and most species have a free-swimming veliger larva. The planktonic larvae of some north-eastern Atlantic and Mediterranean rissoids are important as food for larval herring (Lebour 1934).

Rissoids are found worldwide in shallow seas especially in the mid to lower littoral zones, with a few species in brackish water. Some rissoids live on the continental slopes, but rarely any deeper. They occur on algae and beneath rocks, or under any other object which provides shelter. Generally, species living on algae are highly mobile, with a pigmented head-foot (Fig. 15.108M) and usually a well-developed posterior pedal gland (Fig. 15.108N). Those living under the shelter of stones and similar habitats usually lack a posterior pedal gland and have a translucent-white head and foot.

Species which have a posterior pedal gland typically can secrete threads of mucus on which they can suspend themselves from the surface film.

According to Ponder (1985a), this family comprises 31 valid genera, 15 of which occur in Australia. Some of these have a worldwide distribution (*Manzonina*, *Rissoina*, *Zebina*, *Stosicia*, *Pusillina* and *Alvania*), but a few are essentially Australasian. These are *Attenuata*, *Sriatestea*, *Lironoba*, and *Powellisetia* [this latter genus is also found in the Antarctic and Subantarctic regions (Ponder 1983b) and Chile (Ponder & Worsfold 1994)]. The genus *Onoba* is distributed mainly in temperate and cold regions of both hemispheres. Sleurs (1993) has recently reviewed some members of the genus *Rissoina*, including some Australian taxa.

Presumably because many rissoids tend to inhabit environments that are not favourable for fossilisation, the fossil record for rissoids is rather poor, although better known than that for other rissoidean families. The first known fossils are from the Upper Jurassic of Europe (Ponder 1985a, 1988a). The family is well represented in the Tertiary, but is rarer in Cretaceous rocks. Some of the living genera extend back to the Eocene of southern Australia. Australian Tertiary rissoids are as yet largely undescribed.

Family Epigridae

Epigrids are a small group of marine snails with elongate-oval, smooth shells, up to 6 mm in length. The family is distinguished mainly by the unusual taenioglossate radula.

Members of the genus *Epigrus* were referred to the Rissoidae because of the similarity of their shells to those of various rissoid genera, but Ponder (1985a) established, for them, a separate family based on the very unusual radula.

The shell is smooth, glossy, non-umbilicate and has slightly convex whorls (Fig. 15.109A). The protoconch is smooth, dome-shaped and paucispiral. The aperture is D-shaped and has a simple, continuous peristome. A varix is absent and there is no inner organic layer or obvious periostracum. The operculum is simple, thin and has an eccentric nucleus.

Both the ctenidium and osphradium are present in the mantle cavity and are of similar configuration to those of rissoids.

There is some evidence that *E. cylindraceus* feeds, at least in part, on foraminiferans (Ponder 1985a). The radula is very small and has minute, narrow central teeth which are simple and have only one cusp (Fig. 15.109B). The lateral teeth are rectangular and have several, small blunt cusps, the innermost being slightly larger. The innermost marginal teeth are slightly larger than the lateral teeth and are very short and broad with straight cutting edges parallel to the base. The outer marginal teeth are roughly the same size as the lateral teeth and are subrectangular with a straight cutting edge and small blunt cusps, of which the outermost are the longest.

These snails appear to live among coarse sediments on the continental shelf and in deeper sublittoral areas. Development is probably direct, judging by the morphology of the protoconch. Virtually nothing else is known about their biology. Living material has proved difficult to obtain so little anatomical work has been done.

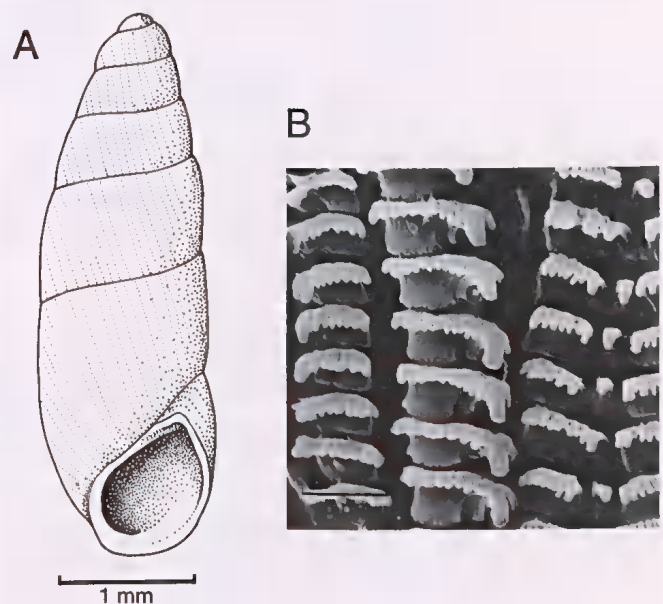


Figure 15.109 Family Epigridae. *Epigrus cylindraceus*: A, shell, apertural view; B, radular teeth on one side of the radula; the narrow central teeth are to the right. [A, S. Weidland; B, W.F. Ponder]

The genus *Epigrus* appears to be indigenous to Australia and is found around the entire Australian coast. At present it comprises only three (possibly four) species and is the only genus in this family. The earliest known fossils are from the Pliocene of South Australia (Ludbrook 1956).

Family Iravadiidae

Iravadiids are small (usually less than 10 mm in length) estuarine and marine snails that have narrowly conic to ovate-conic shells with a smooth, depressed protoconch. The teleoconch is smooth or has predominantly spiral, sometimes clathrate, sculpture. The cephalic tentacles are often ciliated and sometimes have transverse colour bands. Pallial and metapodial tentacles are usually absent, but if present are small, and the foot lacks a posterior pedal gland. The corneous operculum has an eccentric (Fig. 15.110F), submarginal or marginal (Fig. 15.110E) nucleus. The penis is short and thick, often with a swollen distal end, and has accessory glandular structures including apocrine glands in some taxa. The bursa copulatrix is usually pallial (Fig. 15.110J), the female genital system exhibits diverse morphologies (Ponder 1984).

Thiele (1928a) gave *Iravadia* subfamily status in the Hydrobiidae and raised *Fairbankia* to subfamily status in the Northern Hemisphere freshwater family Micromelaniidae. Brandt (1968) included both of these genera in the Iravadiidae, a course followed by Ponder (1984) who reviewed the family and included additional genera previously assigned to several different families. Starobogatov, Sitnikova & Zatravkin (1989) have, with minimal justification, divided the family, as recognised by Ponder (1984), into two, the Hyalidae and Iravadiidae, and in the latter they recognise three subfamilies.

The shell (Fig. 15.110A–C) is typically solid, narrowly conic to ovate-conic and usually nonumbilicate. The protoconch (Fig. 15.110D) is small, smooth, planorboid to depressed dome-shaped, typically with a minute first whorl. The surface of the teleoconch is smooth or predominantly spirally sculptured; axial sculpture is present as growth lines, lamellae or, rarely, as ribs; some shells have clathrate sculpture (Fig. 15.110B). The aperture is oval and weakly to distinctly angled both anteriorly and posteriorly. The peristome is typically somewhat thickened and there is often a broad, strong varix on the outer lip. The periostracum may be well developed and, in a few species, bears processes.

The animals (Fig. 15.110I) are often coloured, mostly with black pigmentation. The cephalic tentacles are long and slender and often bear rings of black pigment. The snout is usually bilobed. The foot is antero-laterally expanded, with the anterior margin indented, and posteriorly either pointed, rounded, slightly indented or deeply bifurcate. One metapodial tentacle (or two in *Lantauia*, Ponder 1994b) is present in a few taxa. There is a well-developed anterior pedal gland, but no posterior pedal gland.

The osphradium is conspicuous, bordered by narrow, ciliated ridges, and is about two thirds the length of the well-developed ctenidium. A hypobranchial gland is present.

Many iravadiids live partially buried in mud or sediment and probably feed on decaying organic matter or bacteria. The alimentary canal is typical of the superfamily. The central radular teeth (Fig. 15.110G, H) are typically short and have several cusps on the cutting edge and zero to four pairs of basal cusps. The lateral teeth each have up to seven cusps and the marginal teeth have many small cusps.

The kidney is a simple sac with a thin lining, except for a renal gland on the outer wall. The nervous system is similar to that of Hydrobiidae and several other related families.

Most iravadiids probably have planktonic veligers as far as can be judged from protoconch morphology and information on the larva of one European species (Thorson 1946). Egg capsules have not been recorded for any member of this family.

Many iravadiids are found either in brackish water, often associated with mangroves, or living in enclosed bays. A few species are entirely marine, living in the lower littoral or sublittoral zones or on the continental shelf (Ponder 1984).

The family occurs virtually worldwide, but most species are found in the Indo-West Pacific. There are no endemic Australian genera, but four of the nine genera recognised occur in Australia (Ponder 1984). These are *Iravadia*, *Chevallieria*, *Nozeba* and *Rissopsis*. *Iravadia*, as recognised by Ponder (1984), contains five subgenera (raised to generic rank by Starobogatov *et al.* 1989), all of which occur in Australia and the Indo-Pacific region, except for the most primitive subgenus, which includes European Tertiary species. A new genus, *Lantauia*, was described recently from Hong Kong (Ponder 1994b). Two species, *I. quadrasi* and *I. mahimensis*, are distributed widely in the Indo-West Pacific and are abundant in tropical mangroves in Australia. *Chevallieria* also has an Indo-Pacific distribution with Tertiary fossils in Europe, Australia (Ponder 1984) and New Zealand (Beu & Maxwell 1990). Recent species of *Nozeba* are found in Australia and New Zealand (as well as in Hong Kong and the Philippines), but Tertiary species have been recognised in Europe, North America and New Zealand. An Upper Cretaceous species in this genus from North America is the earliest known iravadiid (Ponder 1984; Dockery 1993). Species of the fourth genus, *Rissopsis*, are widely distributed in the tropical Indo-Pacific, but are rare in collections.

The ancestral iravadiids may have inhabited sheltered bays and estuaries, with many species later migrating into low salinity areas and other species becoming entirely marine. The genera *Chevallieria* and *Nozeba* are found in Eocene rocks and *Chevallieria* is recorded from the Miocene and Pliocene of Australia (Ponder 1984). All genera occurring as fossils have extant species, except *Rhombostoma* which occurred from the Miocene to the Pliocene of Europe.

Family Hydrobiidae

Hydrobiids are fresh and brackish water snails with elongate to flat-spired shells usually less than 10 mm in maximum length. Shells are usually smooth, but sometimes have spiral sculpture or, rarely, axial ribs or periostracal ridges or spines, and have simple oval to subcircular apertures. The operculum has an eccentric to central nucleus, is horny and with or without white (?calcareous) deposits on its inner side. The cephalic tentacles are long, there is usually no pallial tentacle (rarely a small one on the right side) and never a metapodial tentacle. The foot lacks a posterior pedal gland and the bursa copulatrix is located behind the albumen gland (Fig. 15.111H) and posterior to the mantle cavity.

Hydrobiids are common brackish and freshwater snails and, although they have long been regarded as being distinct from the marine Rissoidae which they resemble superficially, their recognition as a discrete group has had a complex history. Early classifications tended to lump other freshwater (and brackish-water) rissoidae families with the hydrobiids but in the last 15 years some European workers (for example, Radoman, 1973, 1983) have split the family into several smaller family units and have even recognised one (Hydrobioidea) or more separate superfamilies for the group.

Hydrobiid shells (Fig. 15.111A–D) are very diverse in shape, ranging from long and slender to flat spired. Shorter spired shells tend to have an umbilicus, whereas taller spired ones do not. Most Australian species are smooth, only five genera (*Ascorhis*, *Hemistomia*, *Posticobia*, *Austropyrgus* and *Clenchiella*) having species with distinct spiral sculpture. The aperture is simple, ovate to subcircular, and usually lacks an external varix. The protoconch is typically of about one and a half whorls and has a pitted microsculpture, although other, usually simple, types of microsculpture occur. A well-developed periostracum forms a peripheral flange or spines in the New Zealand species *Potamopyrgus antipodarum*, which has been introduced into

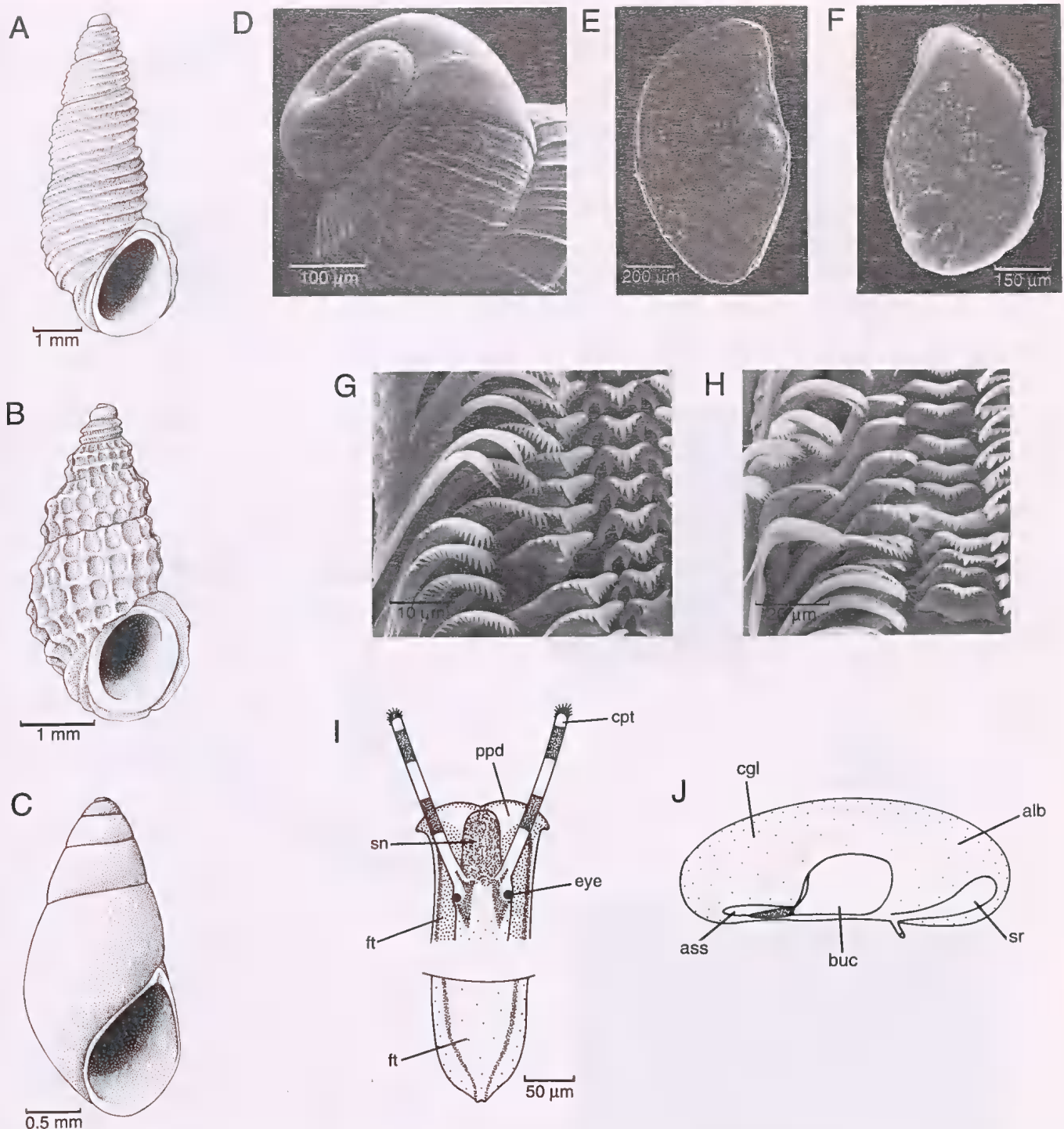


Figure 15.110 Family Irvadiidae. A–C, shells, apertural view: A, *Irvadia (Fairbankia) australis*; B, *Irvadia (Irvadia) quadrasi*; C, *Nozeba topaziaca*. D, *Irvadia (Irvadia) quadrasi*, protoconch. E, F, opercula: E, *Irvadia (Pseudonoba) densilabrum*, outer surface; F, *Nozeba topaziaca*, outer surface. G, H, teeth on one side of radulae: G, *Nozeba topaziaca*; H, *Irvadia (Fairbankia) australis*. I, *Irvadia (Irvadia) quadrasi*, head-foot, dorsal view. J, *Irvadia (Fairbankia) australis*, female reproductive system from left side. alb, albumen gland; ass, anterior sperm sac; buc, bursa copulatrix; cgl, capsule gland; cpt, cephalic tentacle; eye, eye; ft, foot; ppd, propodium; sn, snout; sr, seminal receptacle. (I, J, after Ponder 1984b)

Australia. The operculum is horny, and in some Australasian genera has a white (possibly calcareous) smear on the inner side which, in a few genera, is developed into one to several pegs (Fig. 15.111E).

The head (Fig. 15.111G) has long cephalic tentacles which are inconspicuously ciliated in some species, in others obviously ciliated with short, transverse, ciliated ridges on the proximal part of the left tentacle. The eyes are usually conspicuous and are located in bulges on the outer sides of the tentacles. A small pallial tentacle is present on the right side in a few genera. The large snout is bilobed distally and in one Australian genus (*Ascorhis*) the females have lateral buccal pouches on the snout for storing sand grains (Fig. 15.111G; Ponder & Clark 1988). The simple foot is rounded anteriorly and posteriorly.

The ctenidium is typically well developed (reduced in a few tiny species and lost in a few non-Australian taxa), and is usually much longer than the oval osphradium. A hypobranchial gland is often present.

A pair of jaws is present and the radula (Fig. 15.111F) is typical of the Rissooidea, the central teeth having one to several pairs of basal denticles. The mid-oesophagus has long dorsal folds and the stomach has one or two openings to the digestive gland(s), the second gland, if present, being very small. Food consists of unicellular algae, bacteria and detritus. A number of detailed studies have been carried out on feeding in Northern Hemisphere species of *Hydrobia* (see for example, Lopez & Kofoed 1980; Forbes & Lopez 1989; Levinton & de Witt 1989).

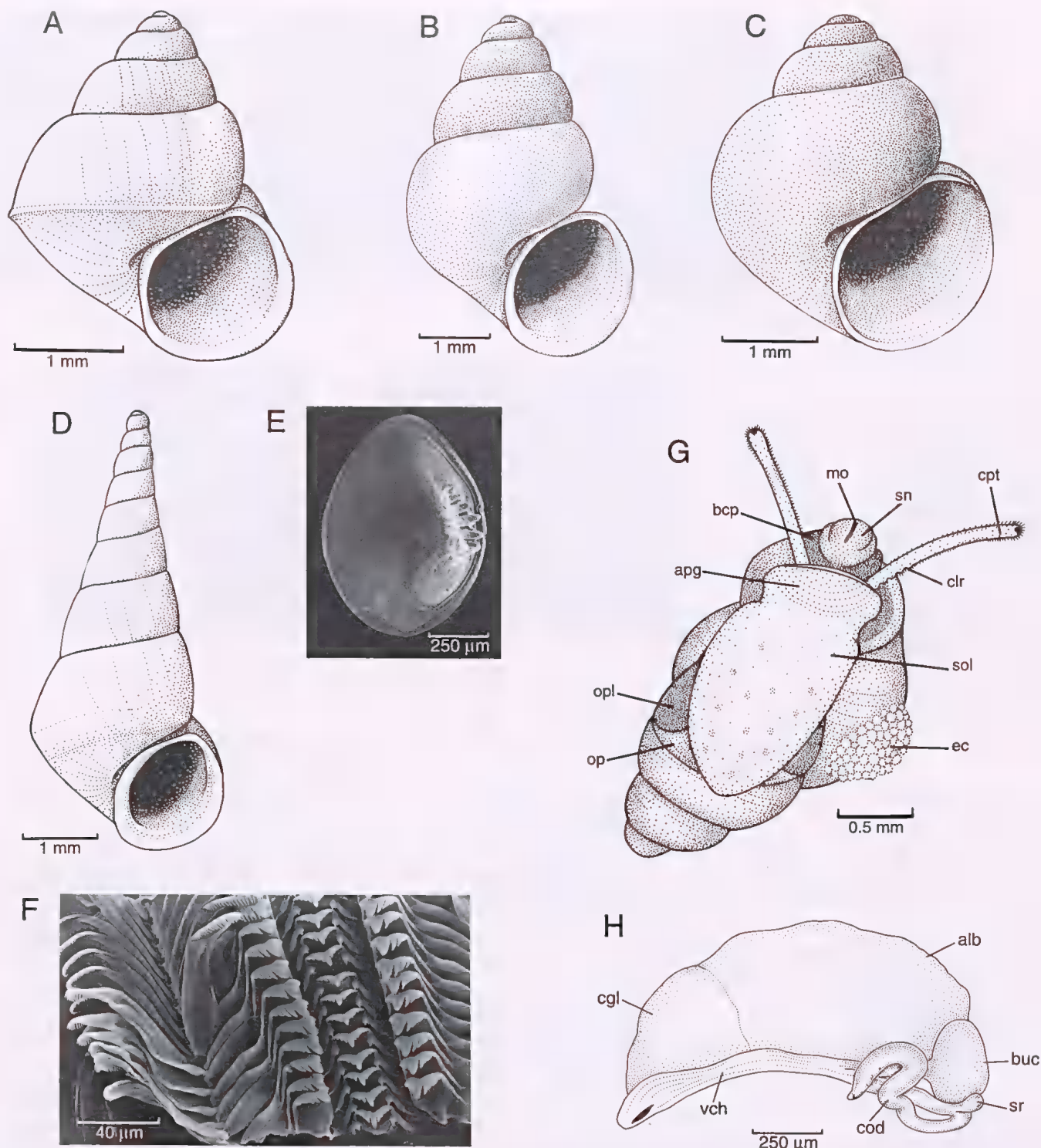


Figure 15.111 Family Hydrobiidae. A–D, shells, apertural view: A, *Posticobia brazieri*; B, *Austropyrgus woodsii*; C, *Beddomeia launcestonensis*; D, *Tatea rufilabris*. E, *Tatea huonensis*, operculum, inner surface. F, *Jardinea thaanumi*, portion of radula showing the central and lateral teeth, and the marginal teeth on the left. G, *Ascorhis tasmanica*, female, ventral view, showing the head-foot and egg capsule. H, *Beddomeia launcestonensis*, female genital system. alb albumen gland; apg, anterior pedal gland; bcp, buccal pouch; buc, bursa copulatrix; cgl, capsule gland; clr, ciliated ridges on left cephalic tentacle; cod, coiled (or renal) oviduct; cpt, cephalic tentacle; ec, egg capsule; mo, mouth; op, operculum; opl, opercular lobe; sn, snout; sol, sole of foot; sr, seminal receptacle; vch, ventral channel. (G, after Ponder & Clark 1989; H, after Ponder *et al.* 1993)

The kidney is thin walled except for the renal gland on the outer wall. The nervous system is typical of that of most rissooideans, and the supra-oesophageal-pleural commissure is longer than the suboesophageal-pleural commissure.

Males have a simple to complexly lobed or glandular penis, some with apocrine glands, although most Australasian hydrobiids have simple penes. The prostate gland is usually closed, but is open in one Australian genus (*Ascorhis*). The female reproductive system is variable in this family (Ponder 1988a) with monaulic and dialic conditions occurring; the normal monaulic condition being typical for Australasian species. The bursa copulatrix is always posterior to the albumen gland and there are usually one to several

seminal receptacles that arise from the coiled 'renal' oviduct (Fig. 15.111H). Egg capsules are usually hemispherical, covered with sand grains or horny. Development is direct in most species but some brackish-water taxa have a veliger larval stage.

Hydrobiids live in a wide variety of habitats from estuarine mudflats to mountain lakes, caves and groundwater, rivers and even desert artesian springs. In the latter habitats they have undergone some spectacular radiations in North America and Mexico and in springs associated with the Great Artesian Basin in South Australia (Ponder 1989b; Ponder, Hershler & Jenkins 1989; Ponder, Egger & Colgan 1995; Ponder, Colgan, Terzis, Clark, & Miller 1996) and Queensland (Ponder 1986a; Ponder & Clark

1990) where there are four genera, three of them endemic, containing more than 20 species (for example, see Fig. 1.70). Several species in the endemic genus *Jardinella*, live in springs in western Queensland (Ponder & Clark 1990), whereas other congeners live in coastal rivers in north-eastern Queensland (Ponder 1991c).

Most Australian hydrobiids are confined to the south-eastern part of Australia, including Tasmania, and a large number of (mainly undescribed) taxa (greater than 150 species) are now known to exist. Most of these live in permanent water bodies such as small streams, springs and seepages; only a few species are found in large streams and rivers. A significant radiation of hydrobiids has been described from Lord Howe Island (Ponder 1982). In some other parts of the world (especially Europe, North America and New Zealand) significant subterranean hydrobiid faunas are known, some living in streams in caves, others in the interstices of gravel in ground water, yet others in limestone aquifers. Many undescribed species are known from caves in Tasmania and one, *Pseudotricula eberhardi*, has been described from caves at Precipitous Bluff, south-western Tasmania (Ponder 1992a). A few (undescribed) species are known from sink holes near Mt Gambier, South Australia, and from caves in New South Wales and the Northern Territory, and it is probable that more subterranean species remain to be discovered. An interstitial species is known from Lord Howe Island (Ponder 1982) and an undescribed species has been found in the Flinders Ranges, South Australia (Cooling & Boulton 1993). A common characteristic of these species is that they lack body pigment and often eye pigment as well. Climo (1974, 1977) has described a significant subterranean and interstitial fauna from New Zealand.

The Australian fauna, although species-rich, comprises relatively few genera. The great majority of species are referable to the genus *Austropyrgus* (Fig. 15.111B), characterised by elongate-conical to broadly conical, usually smooth shells and a pegged operculum. Species of *Austropyrgus*, and the closely related genera *Hemistomia* and *Fluvidona* are now known from southern Queensland to Tasmania and southern Western Australia, New Zealand, Lord Howe Island and New Caledonia (Ponder 1982, 1992b). Species in another closely related genus, *Posticobia* (Fig. 15.111A), known from southern Queensland to South Australia, have broadly conical shells, and some bear a peripheral keel or angulation; they have a strongly pegged operculum. This genus does not occur in Tasmania or the southern part of the south-eastern Australian mainland, however, an extinct species is known from Norfolk Island (Ponder 1981). A complex of several related genera, confined to Tasmania and eastern Victoria, with elongate conical to trochiform shells and a simple, paucispiral operculum, has undergone a major radiation in Tasmania (Ponder *et al.* 1993). This group includes *Beddomeia* (Fig. 15.111C), species of which are all low-spired; the tall-spired genus, *Phrantela*, and *Nanocochlea* from Tasmania; and *Victodrobia*, which is variable in shell shape, from eastern Victoria. Some species of *Beddomeia* resemble some South American taxa and it has been suggested that they are related (see Davis & Pons da Silva 1984) although this is unlikely on the basis of anatomical comparisons (Ponder *et al.* 1993). *Fluviopupa* species are distinguished by having a bilobed penis; they are found on some Pacific Islands (Hubendick 1952; Starmühlner 1976) including New Caledonia (Starmühlner 1970) and Lord Howe Island (Ponder 1982).

The most abundant hydrobiid in much of south-eastern Australia and in Tasmania and South Australia, is the New Zealand *Potamopyrgus antipodarum* (= *niger* or *nigra* of Australian authors), until recently regarded as an Australian native species (see Ponder 1988c). This species is a parthenogenetic brooder (Fig. 15.25) and has a variable, conical shell, often with a peripheral row of periostracal spines or a ridge. It is often found in large numbers, especially in disturbed habitats, and can be a nuisance in water supplies. *Potamopyrgus* often extends into slightly brackish water, but the true brackish-water genera include *Tatea* (Fig. 15.111D) with elongate shells with an angled or

subangled last whorl and a strongly pegged operculum (Ponder, Colgan & Clark 1991), and the smooth-shelled to spirally ridged *Ascorhis* (Fig. 15.111G; see Ponder & Clark 1988), which is not closely related to any other known genus. *Ascorhis* is readily identified from its females which have pouches on the sides of the snout in which they store sand grains used for coating the egg capsules. In tropical Australia, the peculiar, almost planispiral, genus *Clenchiella* is found amongst mangroves.

The Hydrobiidae probably arose in the Jurassic (Ponder 1988a), but generally have a poor fossil record, although many species are known from the European early Tertiary. A few species are known from the Australian Tertiary, including some from the Miocene of the Northern Territory (McMichael 1968) and South Australia (Ludbrook 1980).

The great diversity of hydrobiids is the result of their low vagility. This tends to isolate populations which are, of necessity, confined to permanent water, resulting for some in significant small-scale genetic differentiation (for example Ponder *et al.* 1994). Many species appear to be confined to very small areas, sometimes a single spring or stream and are thus potentially very vulnerable to environmental disturbance (Ponder 1994c). Ninety-three Australian species are listed as vulnerable or endangered in the 1994 IUCN Red Data Book (Groombridge 1994).

Family Pomatiopsidae

Pomatiopsidae are freshwater, amphibious or semi-terrestrial snails with elongate to low-spired shells and a simple operculum. The rather short foot lacks a posterior pedal gland and there are no accessory tentacles. The female reproductive system is diallic (the sperm duct and closed pallial oviduct have separate openings to the mantle cavity), and the bursa copulatrix is located posterior to the mantle cavity. Males have a simple penis with a single duct and no appendages or significant glands. Two subfamilies, Pomatiopsinae and Triculinae, are recognised. The family appears to be closely related to the Truncatellidae and Assimineidae (Ponder 1988a).

Many early workers considered taxa now included in this family to be truncatellids (for example Wenz 1938–1944; Cotton 1959a) or hydrobiids. Iredale (1943) created a new family, Cociellidae, for the only Australian genus *Coxiella*. Macpherson (1957) reviewed the species of *Coxiella*, which she included in the Hydrobiidae. Davis (1979) showed that *Coxiella* is allied to *Pomatiopsis* and its relatives and that the group warrants familial status.

The shells are small (less than 15 mm in length), elongate to short spired and usually dextral. The protoconch is paucispiral, and most pomatiopsids have smooth shells, others are variously sculptured, species of *Coxiella* being smooth or spirally striate (Fig. 15.112A). The aperture is simple and some genera, including *Coxiella*, are decollate. The operculum of *Coxiella* is flat and paucispiral, with a smear of calcareous material (Fig. 15.112B).

The largely amphibious Pomatiopsinae, among them *Coxiella*, have a deep furrow (omniphoric groove) on each side of the head, and a suprapedal fold around the sides of the foot, but these features are not present in the aquatic Triculinae. The cephalic tentacles are short to long with eyes at their outer bases (Fig. 15.112D). Movement is by 'steps' (Pomatiopsinae) or ciliary gliding (Triculinae). The eyes have a cluster of glands above them, giving the effect of an 'eyebrow'. The snout is usually rather long.

Anatomically, the family is similar to Hydrobiidae, differing mainly in details of the female reproductive system. Davis (for example, 1967, 1979) has made major contributions to the family and provided many accounts of pomatiopsid anatomy. The ctenidium is usually well developed (reduced in some terrestrial/semiterrestrial genera) and has numerous filaments. The osphradium is about half the length of the ctenidium. The kidney is large and sac-like.

Like many rissooideans, pomatiopsids probably feed mainly on organic detritus. The alimentary canal is typical of the superfamily. The radula has a central tooth that lacks pronounced lateral angles and has two or more pairs of basal processes (Fig. 15.112C).

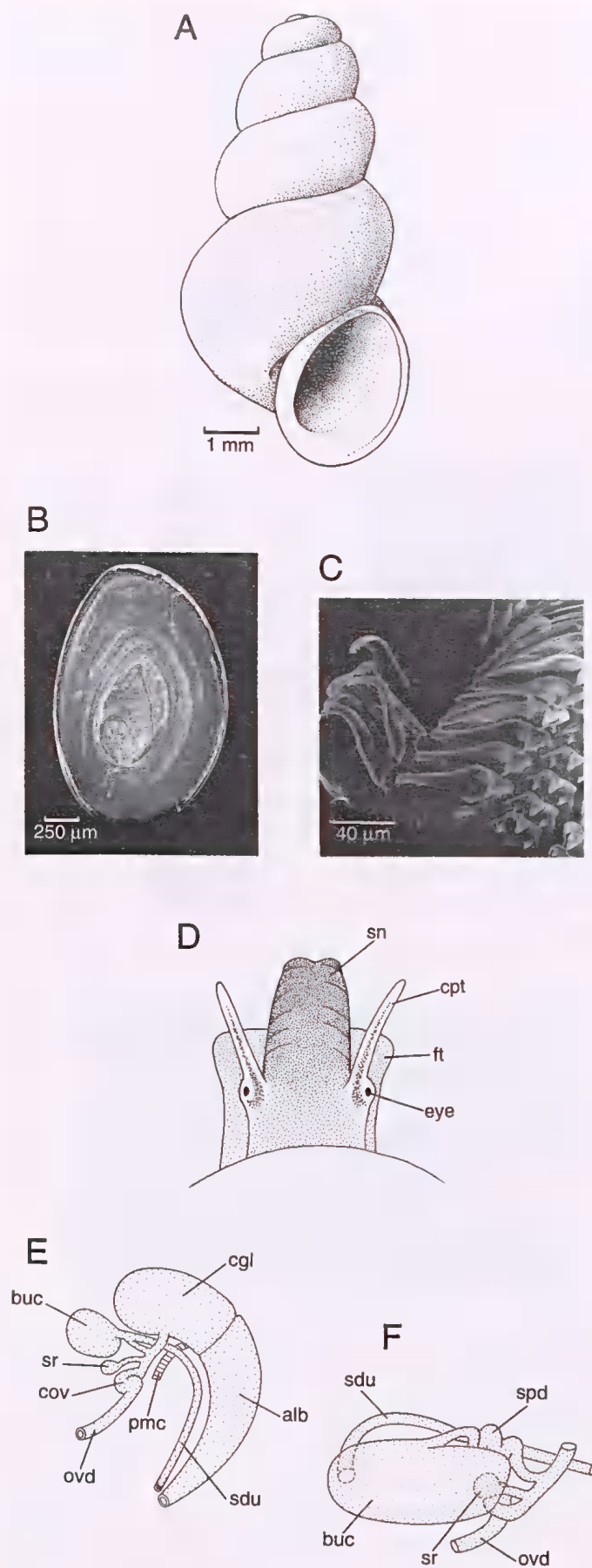


Figure 15.112 Family Pomatiopsidae. A–C, *Coxiella striatula*: A, shell, apertural view; B, operculum; C, teeth on one side of radula. D, *Coxiella* sp., head, dorsal view. E, F, schematic drawings of female reproductive systems: E, subfamily Pomatiopsinae, a generalised system; F, *Coxiella pyrrhostoma*. alb, albumen gland; buc, bursa copulatrix; cgl, capsule gland; cov, coil of oviduct; cpt, cephalic tentacle; eye, eye; ft, foot; ovd, oviduct; pmc, posterior end of the mantle cavity; sdu, spermathecal duct; sn, snout; spd, sperm duct; sr, seminal receptacle. (E, F, after Davis 1979)

[A, D, S. Weidland; B, C, W.F. Ponder; E, F, C. Eadie]

Development is direct in all species. Females are oviparous, depositing eggs singly in capsules coated in sand or mud. The pallial gonoduct of females is separated into a distal capsule gland and a proximal albumen gland (Fig. 15.112E, F). The sperm-receiving duct is separate from the pallial oviduct and has its opening in the mantle cavity. This opening is at the posterior end of the mantle cavity in the Triculinae, and near the anterior end, closely associated with the oviductal opening, in the Pomatiopsinae. Males have a closed prostate gland and the simple penis has a single duct and lacks appendages.

The Asian Triculinae are primarily aquatic, living mostly in freshwater. In the Mekong River the subfamily has undergone a remarkable radiation (Davis 1979) and there is also a significant fauna in China (for example, Davis *et al.* 1986b). The Pomatiopsinae are mostly amphibious and usually live near fresh or brackish water. *Coxiella* lives in hypersaline habitats, primarily salt lakes, and is often extremely abundant, the shells sometimes forming large banks (see Fig. 1.73). It is closely related to the southern African *Tomichia*, species of which occupy a range of habitats and salinities from freshwater to salt lakes (Connolly 1939; Davis 1979, 1981). Most other pomatiopsids live on damp soil or moist vegetation in shaded habitats such as marshes and cliff faces with trickling water.

Some pomatiopsid genera, for example, *Oncomelania* and *Tricula*, are known to be intermediate hosts for blood flukes (*Schistosoma*); none of these occurs in Australasia (see Davis 1980 for a review).

The Australian genus *Coxiella* (= *Coxielladda*) contains ten nominal species, nine from mainland Australia. One, *C. striata*, is also found in Tasmania (Macpherson 1957; Smith 1992). The genus, however, is much in need of revision. Some information on ecology and life history has been provided by Williams & Mellor (1991) who showed that these animals can survive considerable salinity and temperature ranges. The remaining Pomatiopsinae genera are found in North and South America, South Africa and Asia. The Triculinae are found from India and China, through South-East Asia to the Philippines.

The earliest known undoubted pomatiopsid fossils are from the Pleistocene. Pleistocene fossils of *Pomatiopsis* have been found in North America and fossils of *Oncomelania*-like snails, from the same period, have been found in Burma and China (Wenz 1938–1944). Davis (1979) agrees that pomatiopsids originated during the late Jurassic in Gondwana and gave rise, before the Cretaceous breakup of Pangaea, to the two subfamilies. In Australia, *Coxiella* has often been found in Pleistocene and Holocene deposits, but is not known from older deposits.

Family Assimineidae

Assimineids are amphibious snails associated with marine and freshwater or terrestrial environments. They have small ovate to conic shells, no ctenidium, and males have a large penis with no lobes or glandular swellings. The female genital system is monaulic and lacks a ventral channel in the pallial oviduct.

The family Assimineidae was first reviewed by Thiele (1927). R.T. Abbott (1958) investigated *Assimineea* species from the Philippines, and some American and European species have also been studied. Little work has been done on Australian assimineids, but Kershaw (1983) and Solem, Girardi, Slack-Smith & Kendrick (1982) have provided information on the ecology and taxonomy of two species.

Shells (Fig. 15.113A, B) are ovate to moderately conic with smooth, rounded whorls. They are small (less than 10 mm) often with spiral colour bands, threads or grooves. The spire is high to low and the aperture is simple, rounded to ovate and sometimes angled above. The operculum is usually thin, corneous, typically paucispiral with an eccentric nucleus; sometimes a thin calcareous layer is present and occasionally a low projection on the inner side.

The head (Fig. 15.113F) is simple with stubby, rudimentary tentacles in typical assimineids, but the tentacles are long and tapering in the subfamily Omphalotropinae. The foot is short, truncate anteriorly, with a distinct propodium beneath which opens a well-developed anterior pedal gland; there is no posterior pedal gland. Distinct lateral grooves pass down both sides of the neck, these being developed in the terrestrial Omphalotropinae into mucus-carrying gutters with mobile edges. The body colouration is often derived from a combination of black dots and whitish or yellowish granules in the skin. The broad snout is usually distinctly cleft anteriorly. Jaws are usually absent or rudimentary. There is no ctenidium, but the mantle cavity contains a well-developed, crescentic osphradium and a well-developed hypobranchial gland (Marcus, Ev. & Marcus, Er. 1965).

Assimineids are probably primarily detritus feeders, feeding on the organic matter contained in the sediments on which they live (Abbott, R.T. 1958). R.T. Abbott has also observed *Assimineia* feeding on small fragments of meat. The radula (Fig. 15.113C–E) is long and taenioglossate, the central teeth having at least two cusps on each side of the median cusp, and one or more or no pairs of basal cusps. The lateral and inner marginal teeth are simple, the former often having an accessory plate. The outer marginals are typically (but not always) fan-shaped (Fig. 15.113D), finely cuspidate and sometimes with an outer flange.

Males have a simple penis and a closed prostate gland. Females are monaulic, the egg and sperm-conducting channel typically embedded in the capsule gland so that it is surrounded by glandular tissue. The bursa copulatrix and seminal receptacle are located behind the mantle cavity. In at least some species of *Assimineia*, mating occurs out of water with the male crawling upon the shell of the female and extending its long penis into the right side of the mantle cavity of the female (Abbott, R.T. 1958). Egg capsules of *Assimineia* contain a single egg and have a sticky mucous coating which causes mud and detritus to become attached, camouflaging the eggs. These egg capsules are often deposited in groups. The larvae of some assimineids are free-swimming veligers, in other taxa the veliger stage is passed completely within the egg capsule (Abbott, R.T. 1958; Marcus, Ev. & Marcus, Er. 1965; Fowler 1980).

These snails occur worldwide in tropical and temperate regions, generally confined to lowland coastal regions. They are mostly amphibious, spending a great deal of their time out of water. Many assimineids live in the supralittoral zone, although some are associated with freshwater and some species are terrestrial. Many species are estuarine, living among mangroves or in salt marshes, where they are often found crawling over moist mud, rotten logs, stones and leaves. They are mostly nocturnal and negatively phototrophic (Abbott, R.T. 1958) but, like most snails, are active on cloudy and rainy days.

Some Asian species of *Assimineia* are intermediate hosts of the Oriental lung fluke (*Paragonimus westermani*).

The family contains two subfamilies. The Assimineinae comprise several genera, among them the cosmopolitan *Assimineia*, several species of which (mostly unnamed) occur in Australia. Another genus, *Austroassimineia* (see Solem *et al.* 1982), is indigenous to southern Western Australia. Australia appears to be quite depauperate in assimineid genera and species if one refers to the literature, but most of the fauna is undescribed (W.F. Ponder personal observation). Species in the terrestrial subfamily Omphalotropinae are found on many Indo-West Pacific Islands, including Lord Howe Island, and in New Guinea but, strangely, are absent from the Australian mainland.

The earliest known fossil assimineids are from the Miocene of Europe and North America. *Austroassimineia lethia* has been found in the Pleistocene of southern Western Australia. It appears that this is a relict species and probably occurred in coastal seeps and springs in a humid, well-vegetated forest environment in the south-west during the Pleistocene, but now has a restricted distribution (see Solem *et al.* 1982). Even more restricted, undescribed, species

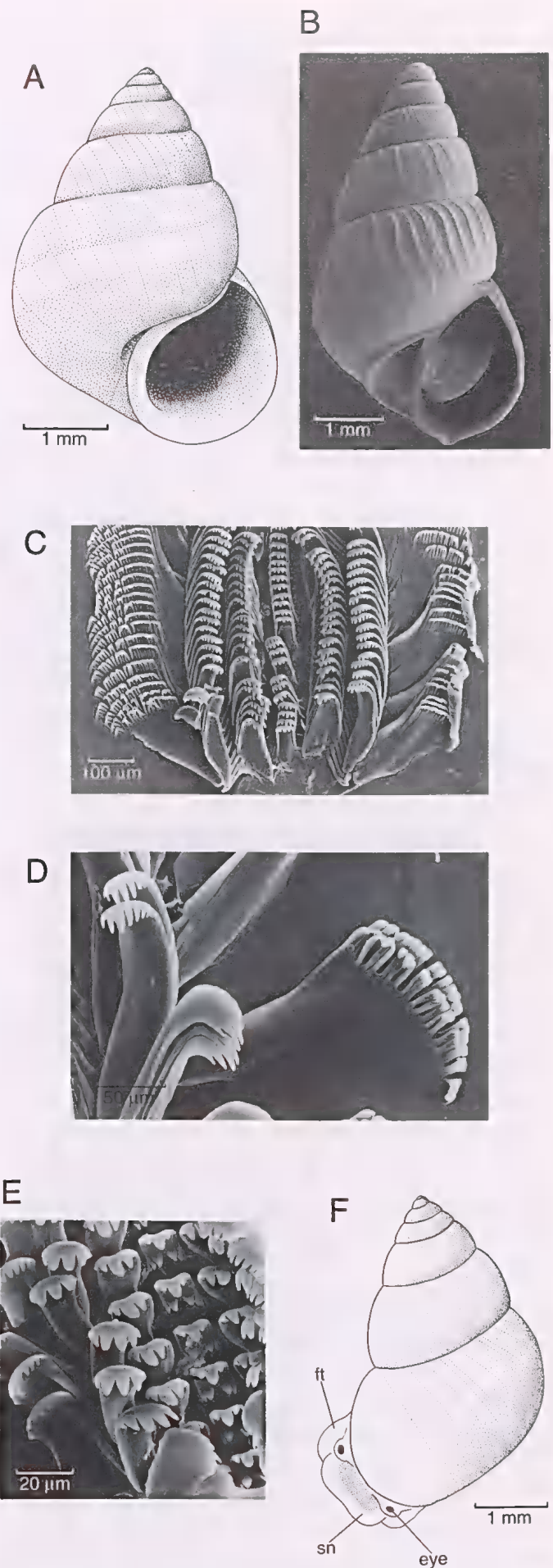


Figure 15.113 Family Assimineidae. A, B, shells, apertural view: A, *Assimineia buccinoides*; B, *Omphalotropis albocarinata*. C–E, portions of radulae: C, D, *Omphalotropis albocarinata*, portion of radula ribbon showing all teeth (C) and details of marginal teeth (D); E, *Assimineia buccinoides* teeth on one side of radula. F, *Assimineia buccinoides*, animal showing head-foot. eye, eye; ft, foot; sn, snout. [A, F, S. Weidland; B–E, W.F. Ponder]

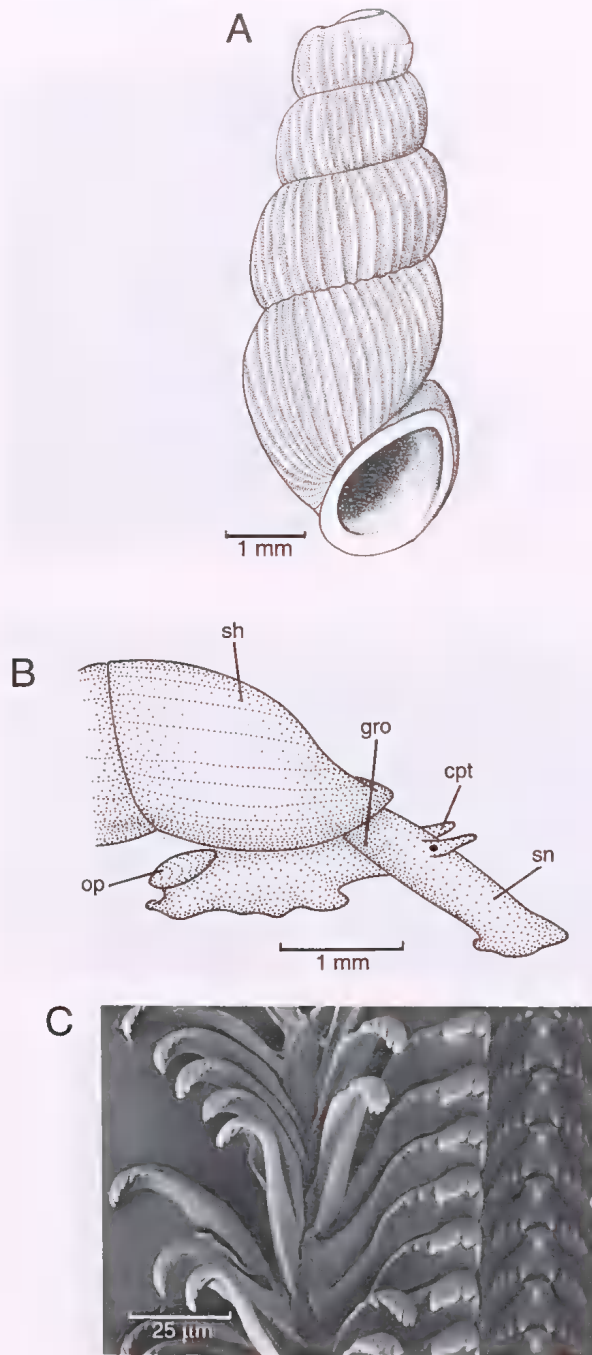


Figure 15.114 Family Truncatellidae. A, *Truncatella scalarina*, shell, apertural view. B, *Truncatella cylindrica*, head-foot, lateral view, showing the proboscis extended. C, *Truncatella scalarina*, teeth on one side of radula. cpt, cephalic tentacle; gro, groove from mantle cavity; op, operculum; sh, shell; sn, snout. (B, after Fretter & Graham 1962)

[A, S. Weidland; B, C. Eadie; C, W.F. Ponder]

occur in north-western and northern Australia – several small aquatic species are found only in isolated spring habitats (W.F. Ponder personal observation).

Family Truncatellidae

These semiterrestrial to terrestrial snails have small (usually less than 10 mm in length but some up to 25 mm) cylindrical, truncate, high-spired and imperforate shells which are smooth or sculptured with axial riblets. They employ a looping method of locomotion by utilising the snout as well as the foot.

Wenz (1938–44) used a broad concept of the family, including in it four 'subfamilies' (among them the Pomatiopsinae) composed of groups no longer regarded as truncatellids. Clench & Turner (1948a) catalogued the family. Davis (1979) provided evidence for separating Pomatiopsidae from the Truncatellidae although Ponder (1988a) maintains a close relationship for these two families.

The cylindrical shells (Fig. 15.114A) are distinctive because adults are decollate through loss of the tapering upper spire whorls. Truncation of the shells is largely mechanical, but must also involve localised shell dissolution. The lumen of the spire whorls is sealed with a calcareous plug. In juveniles, the shell is elongate and many-whorled, but non-truncated, adults are rarely found (Clench & Turner 1948b). The operculum is thin to thick, paucispiral, sometimes has a thin to thick calcareous layer on the outer surface and bears an internal peg in some terrestrial species. There may be forms with smooth and ribbed shells within a single population in some species (Clench & Turner 1948b).

The head (Fig. 15.114B) has short to moderately long, tapering cephalic tentacles, and the snout is long and bears an oral disc. The eyes are situated at the posterior bases and towards the midline of the cephalic tentacles. The foot is short, pedestal-like, with locomotion (out of water) often achieved by looping, first using the oral disc (Fig. 15.114B) and then the foot (Fretter & Graham 1962; see also Seaward 1988).

The mantle cavity contains a reduced ctenidium, a broad osphradium half the length of the ctenidium, and a poorly developed hypobranchial gland (Kosuge 1966b).

Truncatellids probably feed on organic detritus and on small unicellular plants. Their alimentary canal is similar to that of most other rissooideans, although the radula (Fig. 15.114C) is distinctive. The central teeth are triangular, broad-based, unicuspidate, with two or three basal denticles on each side. The lateral teeth have a few large denticles and the marginal teeth are long, with numerous denticles. The kidney is small with a renal gland and the nervous system is rather concentrated (Kosuge 1966b; Rosenberg 1996a).

Little is known about reproduction and life histories. The female has a superficially monaulic reproductive system (Fretter & Graham 1962; Kosuge 1966b), although copulation may possibly occur through the renal opening in some species of *Truncatella* (Ponder 1988a). The egg capsules are globular and development is direct (Fretter & Graham 1978).

Snails of this family live mainly at or just above the high tide line, amongst debris or vegetation in warm temperate and tropical areas. Two genera, *Geomelania* and *Taheitia*, are fully terrestrial, a lifestyle which has evolved independently in several Caribbean species (Rosenberg 1996b). At least three genera can be recognised: the cosmopolitan genus, *Truncatella*, which occurs in Australia, and the genus *Taheitia*, which is known from New Guinea (Turner 1959), but not from Australia. The other terrestrial genus, *Geomelania*, is Caribbean. There are at least two species in southern Australia and a few (revision required) in tropical Australia.

Truncatellids have been found in the Palaeocene in Europe, but because of their ecology, they have a poor fossil record.

Family Elachisinidae

The Elachisinidae, a small group of marine snails, are related to the Irvadiidae and Vitrinellidae and have ovate to ovate-conic shells with a smooth dome-shaped protoconch. They have a metapodial tentacle and a pair of pallial tentacles, but no posterior pedal gland and the posterior part of the foot is bifid. They are also unusual in having the bursa copulatrix located in the pallial roof.

Wenz (1938–1944) placed *Elachisina* in the Naticidae, but later Coan (1964) tentatively included the genus in the Rissoidae. Ponder (1985d), as a result of anatomical studies on the Caribbean species *E. floridanus*, accommodated it in a new family.

The shell (Fig. 15.115A) is small, ovate to ovate-conic, and smooth or spirally sculptured. The protoconch is dome-shaped, paucispiral and smooth. The aperture is large, with a simple peristome, angled anteriorly and posteriorly. The outer lip is prosocline and usually lacks a varix. The operculum is simple, thin, oval and flat and has an eccentric nucleus.

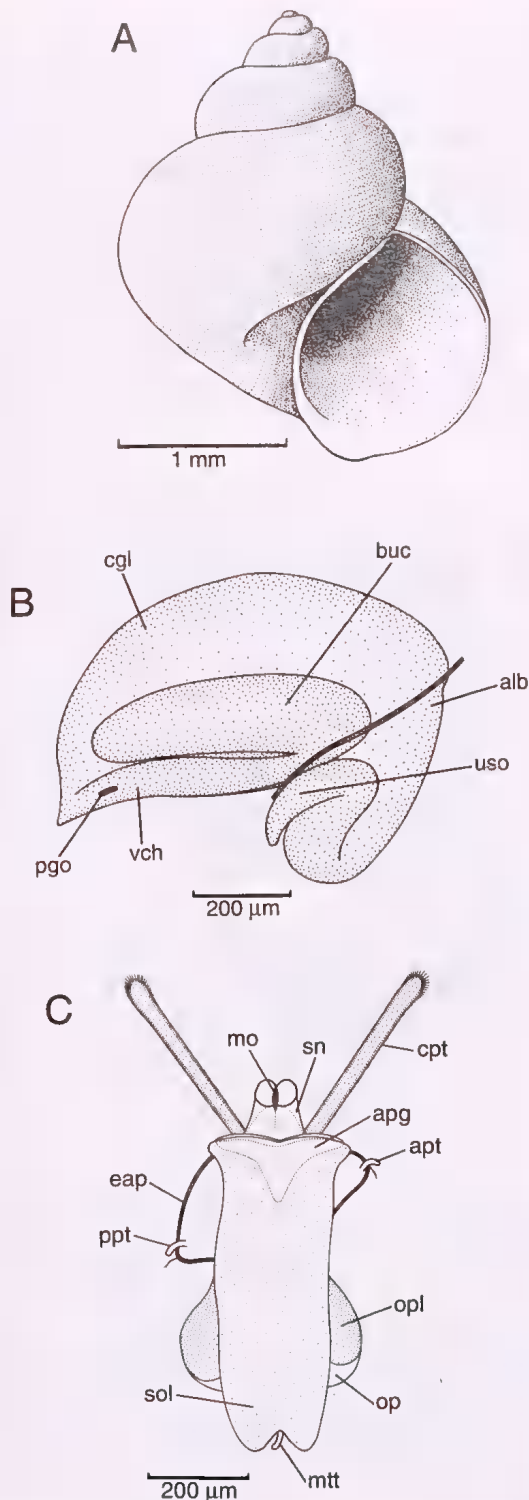


Figure 15.115 Family Elachisinidae. A, *Elachisina* sp., shell, apertural view. B, C, *Elachisina floridana*: B, female reproductive system; C, head-foot, ventral view. alb, albumen gland; apg, anterior pedal gland; apt, anterior pallial tentacle; buc, bursa copulatrix; cgl, capsule gland; cpt, cephalic tentacle; eap, edge of aperture; mo, mouth; mtt, metapodial tentacle; op, operculum; opl, opercular lobe; pgo, pallial genital opening; ppt, posterior pallial tentacle; sn, snout; sol, sole of foot; uso, u-shaped section of oviduct; vch, ventral channel. (B, C, after Ponder 1985c) [A, S. Weidland; B, C, C. Eadie]

The following information is summarised from Ponder (1985d). The head has a bilobed snout and long, slender, ciliated, parallel-sided cephalic tentacles with the eyes on swellings at their outer bases. The foot (Fig. 15.115C) has an anterior pedal gland and a metapodial tentacle arising from its bilobed posterior end. A pallial tentacle is present in the right and left corners of the aperture, or right (posterior) only. The large ctenidium has low, triangular filaments, the oval osphradium being one third its length. A well-developed hypobranchial gland is present.

No direct observations have been made on the feeding habits of species of *Elachisina*. From its stomach contents, *E. floridanus* appears to be a microphagous feeder. The alimentary canal is typical of the superfamily. The central radular teeth have sharp cusps, with the median cusp about twice the length of the marginal cusps. The lateral teeth have a very long shaft, the cutting edge being only slightly more than a quarter of the length of the tooth. The inner marginal teeth have uniform cusps and an almost straight cutting edge that is slightly more than one quarter of the length of the tooth. Cusps on the inner and outer marginal teeth are subequal in size.

The kidney is compact and has a renal gland on the outer wall. The circumoesophageal ganglia are less concentrated than in many other rissooideans.

Larval development is probably direct in most elachisinids, judging from protoconch morphology, but a few have protoconchs, suggesting planktotrophic development. The female reproductive system (Fig. 15.115B) is monaulic, the opening anterior, and there is a bursa copulatrix on the left side of the pallial oviduct, with a U-shaped duct. A pair of posterior seminal receptacles arises from the renal oviduct. The penis has a few glandular lobes and the pallial prostatic gland is open ventrally along most of its length and narrows anteriorly, where it closes over.

Most of the species in this family are found in shallow water, although one undescribed species from the Philippines has been found in 265 m (Ponder 1985d). The New Zealand species, *Elachisina iredalei*, and the Caribbean species, *E. floridanus*, live beneath stones in the intertidal zone (Ponder 1985d).

Elaschisinids are found in tropical eastern North America, western Americas, East Atlantic, Hawaii, Philippines and New Zealand, and undescribed species are known from Australia. Observations by one of us (WFP) on a living specimen of the southern Australian *Dolicrosssea labiata*, a species previously included in the Trochoidea, indicate that it is also an elachisinid.

One species of *Elachisina* is found in Pliocene sediments in Florida, and according to Lozouet (1986), many European Eocene 'lacunids' probably also belong here. He also suggests that *Cirslope* from the Palaeocene of Europe is an elachisinid.

Family Bithyniidae

Bithyniids are small to medium-sized freshwater snails that have a partly calcareous operculum showing concentric growth rings, and a neck lobe on the right side of the head. There are no pallial tentacles, and no metapodial tentacle or posterior pedal gland. The penis has an accessory lobe containing a tubular gland that extends into the cephalic cavity and the kidney extends forwards through much of the mantle roof.

This family was known as Bulimidae prior to the suppression of *Bulimus* by the International Commission on Zoological Nomenclature in favour of *Bithynia* and the current family name Bithyniidae. D.W. Taylor (1966) argued that bithyniids are allied to the Viviparidae in the Ampularioidea. However, any resemblance is due to convergence (Ponder 1988a); sperm morphology (Healy 1988a), the nervous system and the osphradial cytology (Haszprunar 1985a) are typically rissooidean.

Shells are small to medium-sized for the superfamily (sometimes greater than 10 mm in length) ovate to conoidal in shape and rarely have a colour pattern (Fig. 15.116A). Their shells are smooth or have sculpture of spiral lines or ridges, rarely of axial ribs. The aperture is rounded or ovate. The operculum (Fig. 15.116D) is paucispiral, partly calcareous and with concentric growth lines.

The body of the animal is often grey, with black and yellow pigment spots. The tentacles are long, tapering and slender with eyes on slight swellings at their bases (Fig. 15.116B, C). The neck lobe on the right side of the head is at the distal end of a ciliary food groove which passes over the base of the neck region and

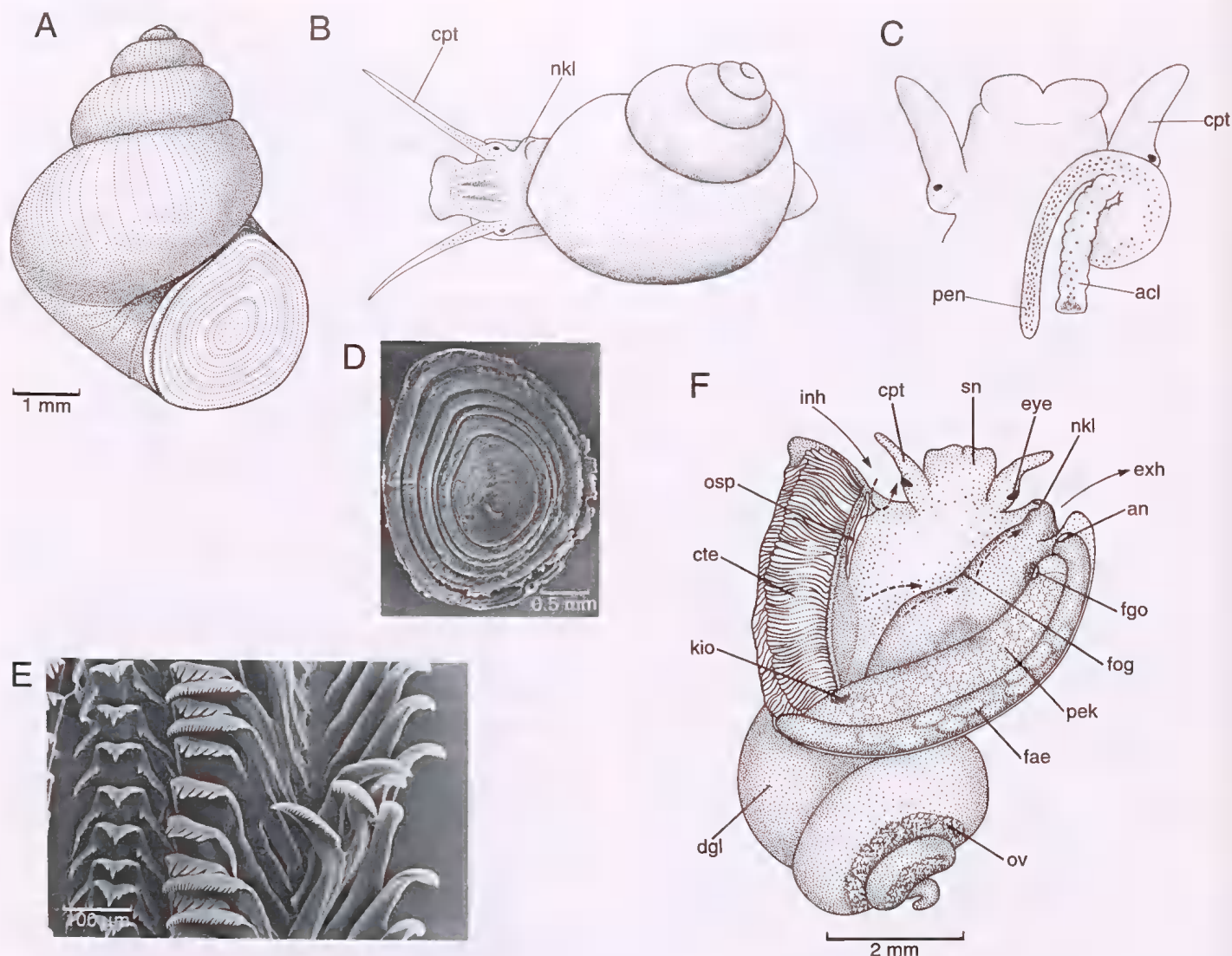


Figure 15.116 Family Bithyniidae. A–E, *Gabbia australis*: A, shell, apertural view, with operculum closing the aperture; B, external appearance of animal showing the head-foot; C, head, dorsal view, showing penis; D, operculum, outer surface; E, teeth on one side of radula. F, *Bithynia tentaculata*, animal removed from shell, the mantle cavity opened dorsally; the continuous arrows show the course of water currents and the broken arrows show the ciliary currents. acl, accessory lobe; an, anus; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; exh, exhalant current; eye, eye; fae, faecal pellets in rectum; fgo, female genital opening; fog, food groove; inh, inhalant current; kio, kidney opening; nkl, neck lobe; osp, osphradium; ov, ovary; pek, pallial extension of kidney; pen, penis; sn, snout. (F, after Fretter & Graham 1962) [A, F. C. Eadie; B, C, S. Weidland; D, E, W.F. Ponder]

collects material from the large ctenidium (Fig. 15.116F). The osphradium is short and situated near the anterior end of the ctenidium (Lilly 1953) and there is a small hypobranchial gland.

These snails are microphagous feeders, ingesting detritus, decaying weed, carrion, diatoms and ruptured plant cells (Lilly 1953; Fretter & Graham 1962). The snout is long and incessantly searches the substratum for food. Food is also collected by the gill in the European species *Bithynia tentaculata*, but the importance of this method of feeding compared to radular feeding in this species (and in other members of the family) is not clear (Schafer 1952; Lilly 1953; Hunter 1957).

The alimentary canal is like that of other rissooideans. The central radular teeth (Fig. 15.116E) have a large middle cusp, numerous lateral cusps and two to six denticles on their bases. The lateral teeth have several cusps on each cutting edge and the marginal teeth have many small cusps. The faecal pellets are elongate, cigar-shaped and spirally grooved.

The kidney has an accessory lobe which extends forward over the genital duct and may act as a reservoir for fluid to keep the ctenidium surface moist during periods of abnormal drying.

Bithyniids have separate sexes. The penis has a long to short, finger-shaped or truncate accessory lobe on the left side, containing an internal tubular gland which extends into the

cephalic haemocoel. The female genital system is generally similar to that of the Hydrobiidae and some other rissooidean families. Egg masses of *B. tentaculata* consist of two parallel rows (rarely three) of interlocking hemispherical capsules (Lilly 1953; Chung 1984). Each capsule contains a single egg embedded in albumen and a dorsal circular plug through which the young snail emerges. Eggs are laid on aquatic vegetation.

These snails live in fresh or slightly brackish water and in Australia are more commonly found in backwaters and billabongs of river systems.

During the summer months, the European *B. tentaculata* is found on water plants on the edges of streams, but during the winter months it buries in the mud at the base of plants (Lilly 1953). The same species can stay out of water for several months, in moist conditions (Lilly 1953). Species of *Gabbia* are found in muddy water and marshy areas and have been observed in arid western Queensland surviving beneath logs and rocks in dried up waterholes, temporary ponds, etc. (W.F. Ponder personal observation).

Some bithyniids are medically important as vectors for Chinese liver fluke (*Clonorchis sinensis*), one of the more significant snail-borne parasites of the Oriental region. There is no naturally occurring population of *C. sinensis* in Australia and experiments carried out to try to infect *Gabbia* species with *C. sinensis* have failed to do so (J. Walker personal communication).

Bithyniids occur in Europe, Africa, Asia, Australia and New Guinea and have been introduced to North America, the Philippines and Indonesia. *Gabbia* is the only bithyniid genus recorded as occurring in Australia, where it is found mainly in the northern parts. Species attributed to this genus are also recorded from New Guinea and South-East Asia. A few nominal species of *Gabbia* are described from Australia, but these are in need of revision; Smith (1992) recognised only one. Some undescribed bithyniids are known to occur in the tropical half of Australia and what may be one species (*Gabbia australis*) is found in the Murray-Darling system (Smith & Kershaw 1979) and in the northern half of New South Wales.

McMichael (1968) reports that *Gabbia* fossils occur in Late Tertiary rocks in the Northern Territory and bithyniids are known from the Neogene of Europe and Egypt (Wenz 1938–1944).

Family Caecidae

Caecids are minute marine snails with shells that are tusk-shaped and tubular (Caecinae) or tubular to depressed trochiform to almost planispiral (Ctiloceratinae). In the Caecinae, adult shells have no protoconch (or rarely so) and the second deciduous stage has the posterior end sealed off by a septum. In the Ctiloceratinae, the long, tubular protoconch is retained. The operculum is circular and multispiral. The cephalic tentacles have long, immobile cilia distally and active cilia along the length of each tentacle. There are no pallial or metapodial tentacles.

This family was originally thought to be related to the Vermetidae, which also have uncoiled shells; it was placed in the Cerithioidea (in which the Vermetidae were previously included). Moore (1962) showed that caecids should be placed in the Rissooidea and that they are related to the Vitrinellidae. Er. Marcus & Ev. Marcus (1963) suggested that the Caecidae are more closely related to the Hydrobiidae than to any other family in the Rissooidea. Ponder (1988a) hypothesised that the Caecidae are an offshoot from the base of the stock that gave rise to the Hydrobiidae, Vitrinellidae, Assimineidae and related families. The Ctiloceratinae of Iredale & Laserson (1957) were provisionally included as a subfamily of the Caecidae by Ponder (1988a) and Ponder & Warén (1988).

The shells of adult Caecinae (Fig. 15.117A, B) are tubular, long, slender and curved. Juvenile shells (Fig. 15.117E) have a smooth, flattened, spiral protoconch which is deciduous. Truncation of the caecine shell occurs twice before the adult form develops (Fig. 15.117E; Götze 1938; Moore 1972a). Firstly the protoconch is lost and later a second stage is discarded and the shell is sealed off by a septum which is often ornamented with a spike or bulge (mucro). The adult shell surface is smooth or transversely (equivalent to axially in a coiled shell) sculptured. The operculum is typically thin, corneous, multispiral and circular, some species having some calcareous material and/or a short peg on the inner side.

The Ctiloceratinae have minute shells (less than 3 mm in length) with a relatively large, smooth, protoconch which is coiled at the apex, the remainder a straight or curved tube (Fig. 15.117C, D, F). The teleoconch is tubular to trochiform or planispiral, with a broad, open umbilicus. It is sculptured with spiral and/or axial ridges, or is smooth. The ctiloceratine animal is essentially unknown. The head-foot of *Parastrophia cygnicollis*, illustrated here for the first time (Fig. 15.117F), and of *P. erseusi* from Western Australia (Hughes, H.P.I. 1993), are similar to those of caecines and represent the only information available.

The Caecinae have a short snout and long, cylindrical cephalic tentacles, with rigid sensory cilia distally and the eyes in bulges at their outer bases (Fig. 15.117G). The left cephalic tentacle has ciliated ridges and has more strongly developed mobile cilia than the right. The foot is short and narrow and, in some species, has a posterior pedal gland. The ctenidium is smaller than the osphradium and has many finger-like filaments (Götze 1938; Moore 1962; Marcus, Er. & Marcus, Ev. 1963).

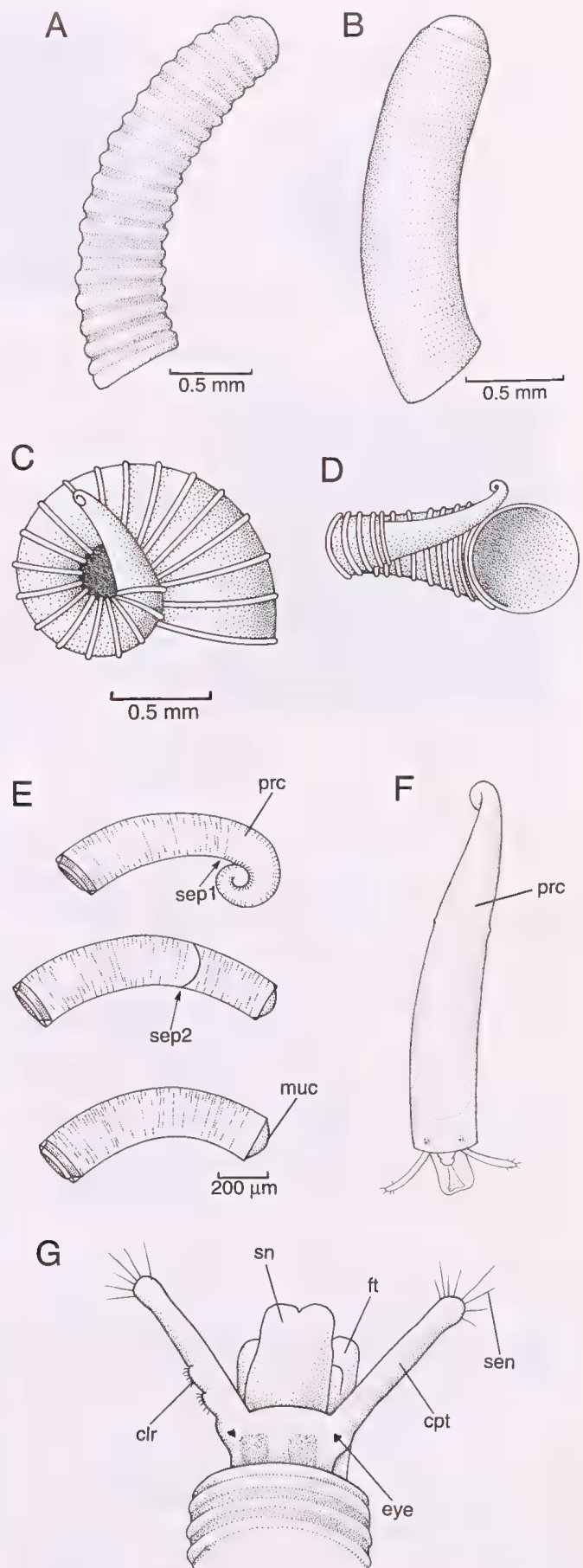


Figure 15.117 Family Caecidae. A–D, shells: A, *Caecum lilianum*; B, *Caecum amputatum*; C, apical view and D, apertural view of *Ctiloceras cyclicum*. E, *Caecum glabrum*, shells at different growth stages, showing the decoliation of the protoconch and the formation of the septum. F, *Parastrophia cygnicollis*, external appearance. G, *Caecum bipartitum*, head, dorsal view. clr, ciliated ridges; cpt, cephalic tentacle; eye, eye; ft, foot; muc, mucro; prc, protoconch; sen, sensory cilia; sep1, septum 1, junction of protoconch and teleoconch; sep2, septum 2; sn, snout. (C, D, after Iredale & Laserson 1957; E, after Götze 1938) [A, B, F, G, S. Weidland; C–E, C. Eadie]

15. PROSOBRANCHS

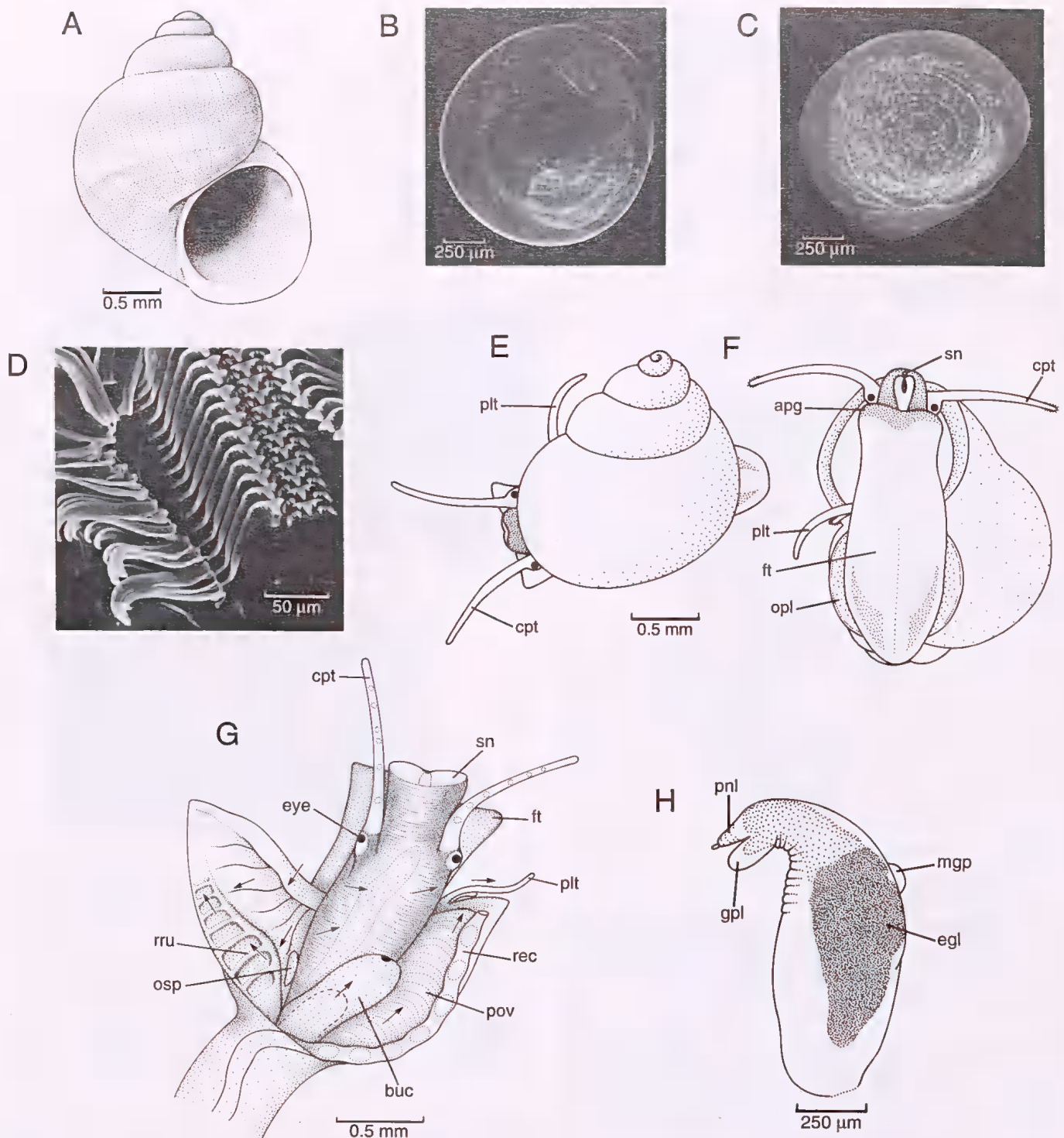


Figure 15.118 Family Hydrococcidae. *Hydrococcus brazieri*: A, shell, apertural view; B, operculum, inner surface; C, operculum, outer surface; D, portion of radula showing teeth on one side; E, animal, dorsal view; F, animal, ventral view; G, female, dorsal view, with the mantle cavity opened, arrows indicate direction of ciliary movement and the broken line indicates the size of an empty bursa copulatrix; H, penis. **apg**, anterior pedal gland; **buc**, bursa copulatrix; **cpt**, cephalic tentacle; **egl**, epithelial gland cells; **eye**, eye; **ft**, foot; **gpl**, glandular penial lobe; **mgl**, median glandular penial lobe; **opl**, opercular lobe; **osp**, osphradium; **plt**, pallial tentacle; **pnl**, terminal part of penis bearing penial duct; **pov**, pallial oviduct; **rec**, rectum; **rru**, respiratory rugae; **sn**, snout. (E–H, after Ponder 1980)

[A, S. Weidland; B–D, W.F. Ponder; E–H, C. Eadie]

Caecines are microphagous feeders with an alimentary canal similar to that of other rissooideans (Götze 1938; Marcus, Er. & Marcus, Ev. 1963). The radula has central teeth with lateral wings, a single pair of basal processes and numerous small cusps on the cutting edge. The inner marginal teeth have larger cusps than the lateral teeth.

The penis often has elaborate penial glands including apocrine glands (Marcus, Er. & Marcus, Ev. 1963) and is usually coiled. The female has a large anteriorly placed bursa copulatrix but otherwise the reproductive tract is typically rissooidean. Larvae are free swimming pelagic veligers and have a tiny, spirally coiled protoconch. The egg capsules of *Caecum corneum* and

C. pulchellum, both from Brazil, are spherical green-brown and covered in detritus such as sand grains and microalgae (Marcus, Er. & Marcus, Ev. 1963).

Caecines inhabit tropical and temperate seas throughout the world. They are found in shallow water, rarely in deeper water. They live on a variety of substrata including algae and seagrasses, beneath rocks and rubble and interstitially in gravel, sometimes on intertidal beaches (Ponder 1990a). Ctiloceratinae are rare and occur in the Caribbean, Mediterranean and the Indo-West Pacific. The largest known fauna occurs in tropical Australia (Iredale & Laseyron 1957). Nearly all species have never been collected alive.

There are about 12 genera and approximately 300 species (Boss 1982) in the Caecinae. The genus *Caecum* is very widespread, and although only about eight species are recorded from Australia, the fauna is certainly larger. More than one genus is represented in Australia, although not recorded in the literature; the Australian species of this family have never been revised, the last major revision of the group being that of de Folin (1875). In the subfamily Ctiloceratinae, ten genera and at least 16 species are recognised in Australia; two of the species were left unnamed by Iredale & Laseron (1957).

Caecids are known from the fossil record to have been in the Tethys Sea during the Cretaceous and may have migrated to the west coast of the Americas by at least the Late Cretaceous (Ponder 1988a). They are found in Late Eocene-Early Oligocene rocks in the Antarctic Peninsula (Zinsmeister 1982). *Strebloceras* is recorded from the Early Eocene of New Zealand (Beu & Maxwell 1990).

Family Hydrococcidae

This monotypic family of small estuarine snails is indigenous to southern and western Australia. Hydrococcids have ovate to ovate-conic, narrowly umbilicate shells and the operculum is circular with a central nucleus. A long, bifid posterior pallial tentacle is present, but there is no ctenidium or clearly defined hypobranchial gland. The penis has glandular lobes and the female genital system is diaulic.

Thiele (1928a) placed *Hydrococcus* in its own subfamily (Hydrococcinae) in the Hydrobiidae. Wenz (1938–1944) was the first to put this monotypic genus in its own family. It has generally been regarded as a family since Wenz's work, although Iredale (1943) and Boss (1982) included *Hydrococcus* in the Bithyniidae. Ponder (1980b) provided the first substantial evidence for the familial status of this group, showing that it is anatomically distinct from other rissooideans. Most of the following account is based on that paper.

The shell is small (up to 4 mm in length), solid, turbinate to conical (Fig. 15.118A). The protoconch is small, smooth and consists of about one and a half whorls. There are four to five moderately convex to strongly convex whorls and the aperture is simple and subcircular. The operculum (Fig. 15.118B, C) is thin, horny and subcircular, with a central nucleus.

The head (Fig. 15.118E–G) has a pair of long, gradually tapering ciliated cephalic tentacles with eyes on bulges at their outer bases. The snout is broad, distally bilobed and black, except for the unpigmented tip. There is a bifid, ciliated pallial tentacle, but no metapodial tentacle. The foot is short, broad, rounded posteriorly, laterally extended anteriorly and lacks a posterior pedal gland. There is no ctenidium or hypobranchial gland and the osphradium is short.

Hydrococcus is probably a general microphagous detritus feeder and its alimentary canal is typical of the superfamily. The central teeth of the radula (Fig. 15.118D) have lateral wings, few cusps and two pairs of basal denticles. The lateral teeth have long outer extensions and a short, inner cutting edge of several cusps. Both the inner and outer marginal teeth are long, narrow, curved distally and have numerous small cusps. The large, thin-walled kidney has a renal gland on its outer wall.

The female reproductive system is diaulic, there being a large pallial bursa copulatrix (Fig. 15.118G) with a separate opening to the mantle cavity. Males have a large penis (Fig. 15.118H) bearing two distal lobes and one small median lobe. Egg capsules of *Hydrococcus brazieri* are deposited on any hard substratum, most often on shells of other individuals or on other living molluscs, dead shells or rocks. The capsules are lens-shaped, transparent and composed of sand cemented together. One embryo develops in each capsule and there are no nurse eggs. Development is direct (Wells & Threlfall 1982a).

The only known species, *Hydrococcus brazieri*, is found living on intertidal flats, often in somewhat brackish water, in estuaries, sheltered bays and lagoons along the southern and western coast of Australia. It is capable of activity in a wide range of salinities and temperatures (Wells & Threlfall 1982b). It is locally very abundant and is most common in mid-littoral sand or muddy-sand flats associated with *Zostera* meadows at or near the mouths of estuaries, deep bays, inlets or sheltered waters (Kershaw 1983; Wells & Threlfall 1981). *Hydrococcus brazieri* is easily confused with *Assimineia buccinoides*, with which it lives in south-eastern Australia; Smith & Kershaw (1979) treated them as synonyms. The features that distinguish these two species are discussed in detail by Kershaw (1983).

Fossil *Hydrococcus* are common in the Pliocene and Pleistocene of southern Western Australia.

Family Vitrinellidae

The Vitrinellidae encompass a heterogeneous assemblage of small marine to brackish-water snails. The shells (Fig. 15.119A–I) have a depressed to flat spire, a simple, usually circular aperture and are umbilicate. The shell is smooth or predominantly spirally sculptured, any axial elements usually being confined to the base or sutural area. Clathrate sculpture is sometimes present and nodules occur in some species. The protoconch is typically multispiral and smooth or almost smooth. The operculum is circular with a central nucleus. A pair of posterior pallial tentacles is usually present and, sometimes, a metapodial tentacle. A posterior pedal gland is absent. This poorly known family is unusual in having at least one species that is a protandrous hermaphrodite and a few species known to live in commensal relationships.

The vitrinellid shell shape is convergent with that of the trochoidean family Skeneidae and some lower heterobranch families (for example Orbitestellidae), resulting in incorrect familial placement of some genera. To date, the only attempts to delineate the family are those of Moore (1972b), Bieler & Mikkelsen (1988) and Ponder (1994b). The heterogeneous nature of the Vitrinellidae has been discussed by Bieler & Mikkelsen (1988) and Ponder (1988a, 1994b). Another family, Tornidae (see Graham 1982), has not been recognised in Australia, and may not be separable from Vitrinellidae (Ponder 1994b).

The following anatomical information is mainly from Fretter (1956), Bieler & Mikkelsen (1988) and Ponder (1994b). The head (Fig. 15.119I) has long, strap-like cephalic tentacles, bearing long stationary 'setae' on the distal ends and with the eyes in bulges at their outer bases. The snout is long and bilobed distally and the anterior end of the foot is expanded into small lateral projections. Posteriorly, the foot is either indented or rounded, often with a metapodial tentacle dorsally, and there is no posterior pedal gland. The mantle edge bears a pair of pallial tentacles on the right side and a single one on the left. The ctenidium is well developed and sometimes has the anterior end free and capable of projecting from the mantle cavity. The osphradium is long and narrow.

Paired jaws are present and the radula (Fig. 15.119J) is of the typical rissooidean form, the central teeth having a single pair of basal denticles. One American species (*Cyclostremiscus beaulti*; Bieler & Mikkelsen 1988) is unusual amongst Rissooidea in having, in some individuals, the salivary glands passing through the nerve ring. The mid-oesophagus lacks any accessory glands and has long dorsal folds. The stomach is large and has a crystalline style; a long posterior caecum is present in some species. The digestive gland has a single opening. Food consists of single-celled algae, bacteria and detritus.

The kidney is large with a renal gland on the outer wall. The nervous system is typical of the superfamily, the connective to the supra-oesophageal ganglion being longer than that to the suboesophageal ganglion.

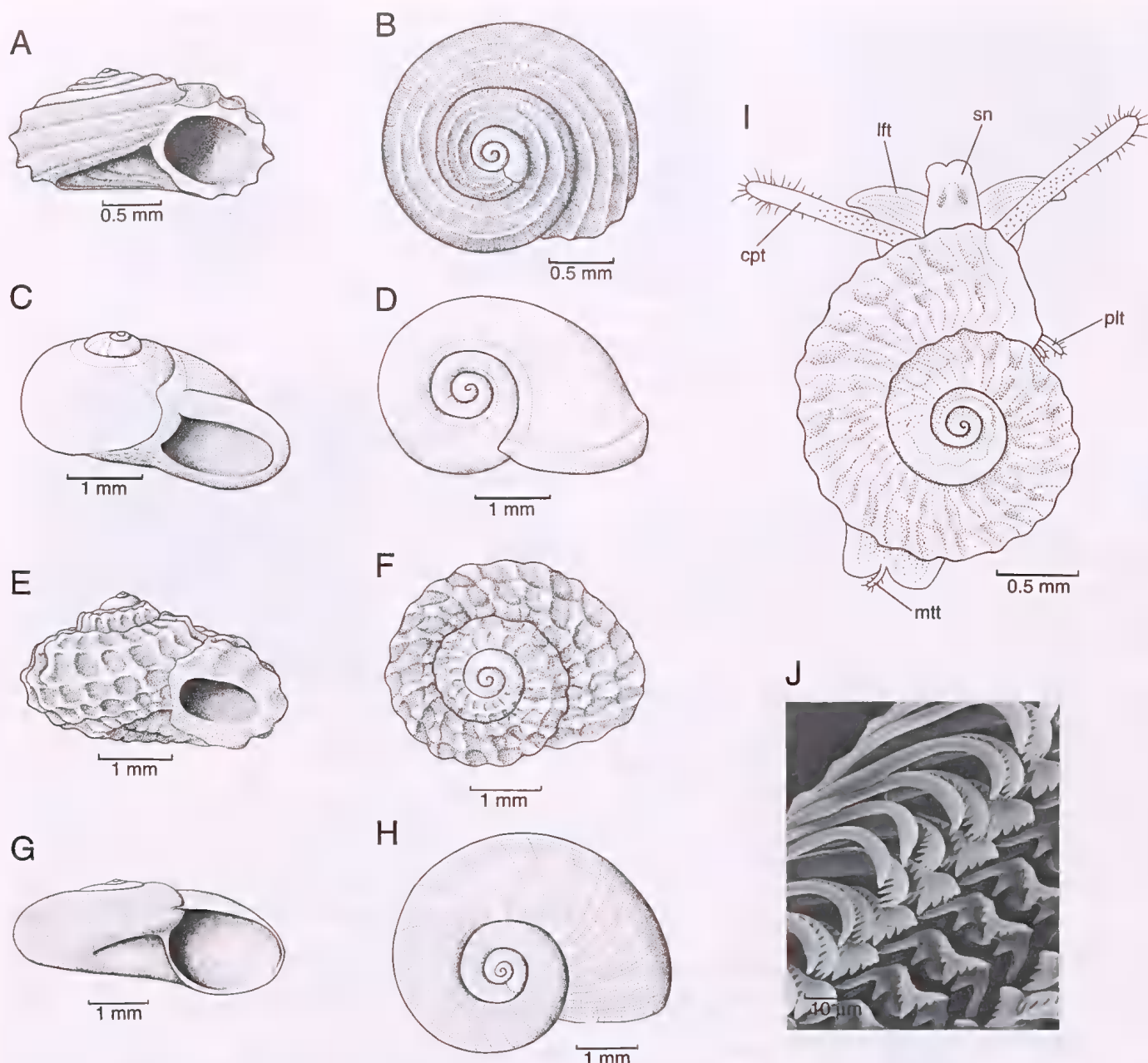


Figure 15.119 Family Vitrinellidae. A–H, shells, apertural and apical view: A, B, *Circulus cingulifera*; C, D, *Teinostoma lucida*; E, F, *Pseudoliotia micans*; G, H, *Sigareturnus planus*. I, *Pseudoliotia speciosa*, animal, dorsal view. J, *Pseudoliotia micans*, teeth on one side of radula. A, C, E, G, shell, apertural view; B, D, F, H, shells, apical view. cpt, cephalic tentacle; lft, lateral projection of foot; mtt, metapodial tentacle; plt, pallial tentacle; sn, snout.

[A–I, S. Weidland; J, W.F. Ponder]

The male has a large, simple penis (with glandular lobes and/or apocrine glands in some Australasian species; Ponder 1988a, personal observation) and the prostate gland is open ventrally to the mantle cavity (Ponder 1994b). The female system has the bursa copulatrix on the left side of the anterior end of the capsule gland (which opens near its posterior end), a coiled, simple to swollen renal oviduct and one to two seminal receptacles. *Cyclostremiscus beaulti* is a protandrous hermaphrodite (Bieler & Mikkelsen 1988), the only recorded occurrence of protandry in the Rissooidea. The eggs of only three species are known. *Circulus texanus* has capsules laid in groups of one to five, each with a sticky gelatinous wall enclosing a single egg (Bieler & Mikkelsen 1988). Veliger larvae are released in this species and presumably in most other vitrinellid species with a multispiral protoconch. *Sigareturnus planus* has lenticular capsules covered with sand grains and *Circulus mortoni* has simple, horny, lenticular capsules (Ponder 1994b).

Some vitrinellids are free living, for example the common Australian species of *Pseudoliotia* which are found living on seagrasses and on hard objects (wood, stones) in estuaries. Some live beneath deeply embedded rocks and a few species are known

to be commensal with burrowing invertebrates. The large Indo-Pacific species, *Sigareturnus planus*, lives in echiurid burrows on intertidal mudflats (Morton, B. & Morton 1983; Morton, B. 1988; Ponder 1994b from Hong Kong; R.C. Willan & W.F. Ponder personal observation from Queensland). The American species *Cochliolepis parasitica* lives with the scale worm *Polydonte lupina* (Moore 1972b) and *Cyclostremiscus beaulti* and *Circulus texanus* in the burrows of the stomatopod crustacean *Lysiosquilla scabricauda* (Bieler & Mikkelsen 1988).

Species presently included in the Vitrinellidae occur in temperate to tropical seas worldwide. The majority of species are found in tropical and subtropical parts of the Americas and the Indo-Pacific. There is a rich fauna in tropical Australia, but few species in temperate Australia, although *Elachorhis tatei*, *Lodderia lodderae* and *Pseudoliotia micans* are common in that area.

This 'family' is in such a state of taxonomic chaos that any discussion of even the genera present in Australia is premature. However, a few common genera can be identified. Species of *Pseudoliotia* (Fig. 15.119E, F, I) are probably the most common Australian vitrinellids, these species being recognised by their

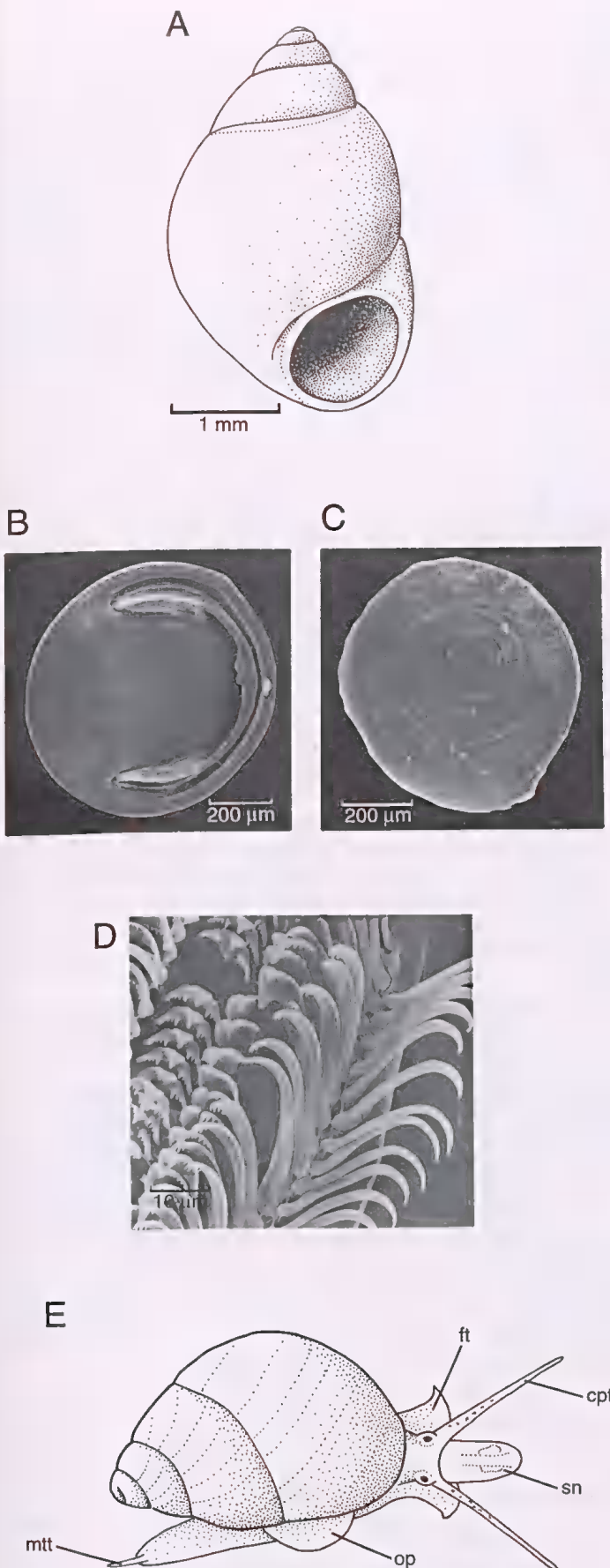


Figure 15.120 Family Stenothyridae. A, *Stenothyra australis*, shell, apertural view. B–E, *Stenothyra* sp.: B, operculum, inner surface; C, operculum, outer surface; D, teeth on one side of radula; E, external appearance of live animal. cpt, cephalic tentacle; ft, foot; mtt, metapodial tentacle; op, operculum; sn, snout. [A, E, S. Weidland; B–D, W.F. Ponder]

nodulose clathrate sculpture. Species of *Circulus* (?= *Elachorbis*) (Fig. 15.119A, B) and *Lodderia* are recognised by their spiral sculpture and there are several common Australian species that could be placed in the former genus. Some Australian species that have smooth shells with a narrow umbilicus bearing a ridge or flange are very similar to true *Vitrinella*, but whether or not they are really related requires confirmation. *Sigaretornus* (Fig. 15.119G, H) contains one species distinguished by its large shell with a large last whorl, wide, simple umbilicus and fine spiral striae. *Teinostoma sensu lato* (Fig. 15.119C, D) is represented by several species distinguished by their solid shells, typically with callus filling the small umbilicus, the shell surface spirally sculptured or smooth. Some *Teinostoma*-like species are rissoideans and others are known to be trochoideans (W.F. Ponder personal observation). Many of the available generic names are based on species that have never been collected alive; without information on the animals their relationships will continue to be questionable. Most Australian species are known only from shells and many remain undescribed.

Convergence in shell characters of this family and other groups makes statements about early vitrinellid fossil history dubious. There are, however, species similar to *Teinostoma* in the Upper Cretaceous of North America and others attributed to the family occur in Tertiary deposits in many parts of the world, commencing in the Palaeocene.

Family Stenothyridae

These fresh and brackish water snails typically have dorso-ventrally compressed shells with a circular aperture. The operculum is unusual in having two keel-like projections on the inner surface. Shells are often sculptured with spiral rows of minute pits, and the pointed posterior foot bears a metapodial tentacle.

Members of this family were originally placed in other families including the Littorinidae, Viviparidae, Rissoidae and Hydrobiidae. Following Wenz's (1938–1944) assignment of family status to this group, they have been regarded as a distinct family although anatomical confirmation has only been produced recently by Kosuge (1969), Davis, Yuan Hua Guo, Hoagland, Ling Cai Zheng, Hong Mu Yang & Yuang Fan Zhou (1986a) and Davis, Chen, Xing & Wu (1988).

Shells (Fig. 15.120A) are small (less than 10 mm long), vary in shape from ovoid to conic or pupoid and have a large last whorl which is often bossed on the left side and/or is compressed dorso-ventrally. The distinctive aperture is circular to subcircular and the peristome is barely thickened. The surface is usually smooth, and sculpture, when present, is never prominent and often consists of spiral rows of small punctuations or delicate grooves. The periostracum is usually well developed and the operculum (Fig. 15.120B, C) is thick, corneous and paucispiral, the inner surface having a low ridge parallel to the outer margin and two short, prominent ridges at each end (Fig. 15.120B).

The cephalic tentacles (Fig. 15.120E) are long, with eyes at their outer bases. The foot is long and narrow, the anterior end with somewhat expanded corners, the posterior end pointed and with an often upwardly projecting metapodial tentacle on its mid-dorsal surface (Fig. 15.120E). The snout is long, cylindrical and often bilobed distally. The body is usually pigmented with black or grey, often with yellowish or orange patches. The osphradium is about half the length of the well-developed ctenidium, which has numerous triangular filaments. The hypobranchial gland is small and not well developed (Davis *et al.* 1986a).

Stenothyrids probably feed on decaying organic matter. The alimentary canal is similar to those of most other rissoidean families. The broad central tooth has an enlarged central cusp with three to six basal cusps on each side and several cusps the cutting edge. The lateral and marginal teeth are typically rissoidean (Fig. 15.120D).

15. PROSOBRANCHS

The egg capsules are sessile, relatively large and few (Annandale & Prashad 1921). The female reproductive system is diaulic with the spermathecal opening at the posterior end of the mantle cavity. The penis is simple (although sometimes with a stylet), and the male has a closed prostate gland (Kosuge 1969; Davis *et al.* 1986a, 1988).

Stenothyrids live in brackish to freshwater, one species even being found in hot springs in Japan. Some species are found in shallow water on the shores of lakes on a variety of hard or soft substrata, including vegetation. Some Asian species live in fast-flowing rivers but no stenothyrids are known from Australia in this habitat. Most Australian species live in slow-flowing water or still water in coastal situations, such as tidal estuaries or small creeks, or in pools in mangroves (W.F. Ponder personal observation).

The latitudinal extant distribution of this family is from India to Japan, with numerous species occurring in Thailand (Mekong River), China and the Philippines. There are also some species in Indonesia, New Guinea, the Pacific islands and the northern half of Australia (Annandale & Prashad 1921; Kuroda 1962; Kosuge 1969; Hoagland & Davis 1979; Davis *et al.* 1986a, 1988). The family comprises two Recent genera, *Stenothyra* and *Gangetia*. *Stenothyra* is the larger genus with more than 40 named species, many of which have restricted distributions, particularly the freshwater species. There are at least 12 Australian species, almost all unnamed (W.F. Ponder personal observation). *Gangetia*, a poorly understood genus, is not known from Australia.

The oldest fossils of this family are from the Palaeocene of Europe. There are several fossil species of *Stenothyra*, but many of the European fossil taxa are now included in *Stenothyrella* (Lozouet 1985).

Superfamily STROMBOIDEA

Shells of stromboideans are medium to very large (20–400 mm) with low to high spires, and the outer lip frequently expanded outwards, sometimes with long spines. The aperture is usually channelled at the anterior end, often with a prolonged columella, and a second notch for one of the eyes. The operculum has a terminal nucleus. The foot is frequently divided transversely. The snout is long. The radula has central teeth each with a pointed, cuspidate cutting edge, broad lateral teeth, and the inner and outer marginal teeth are pointed, elongate and narrow. There is no oesophageal gland (Thiele 1929–1935; Boss 1982) and the stomach has a crystalline style.

The Stromboidea is a small, exclusively marine, largely shallow-water, superfamily comprising only three families, the Strombidae, Struthiolariidae and Aporrhaidae, and about 80 species worldwide. The Strombidae and Struthiolariidae occur in Australian waters. The Aporrhaidae have a long fossil history, but are represented by only the single extant genus, *Aporrhais*, with about five species, restricted to the Atlantic and the Mediterranean. The family Xenophoridae, previously included in the Stromboidea, is now included in a separate superfamily, the Xenophoroidea (Ponder 1983c).

J.E. Morton (1950) discussed relationships within the Stromboidea. Based on shell and anatomical characters, he concluded that the ancestral form must have been similar to modern aporrhoids except that it crawled on the surface of sand or mud and was not adapted for burrowing. This deposit-feeding ancestor gave rise separately to modern Strombidae and Struthiolariidae. The aporrhaid–struthiolariid line became burrowers with the ability to form an inhalant tube using the extensible proboscis-like snout. The pharynx and radula were reduced as an adaptation to suspension-feeding. Specialisations in Strombidae include the modified digestive system, the herbivorous feeding habit and modifications of the external anatomy of the female reproductive system.

Family Strombidae

Strombid shells are medium-sized to very large, reaching 400 mm in length, and low-spired to conical, smooth or sculptured, with long, narrow apertures (Fig. 15.121A–C). The outer lip is frequently flared out, sometimes with long spines, and the columellar end has a channel-shaped process. The operculum is elongate, the snout is long and thin, and the eyes are on long stalks. The foot is narrow and strongly muscular. The osphradium is long and narrow. Sexes are separate (Thiele 1929–1935; Abbott, R.T. 1960; Little 1965c; Franc 1968; Boss 1982).

This family is the largest among the extant Stromboidea. The Indo-Pacific species were investigated in detail by R.T. Abbott (1960, 1961, 1967), who included considerable information on the species occurring in Australian waters and their ranges. In a more recent review of the group, Walls (1980) listed 72 extant species worldwide. The family was also monographed by Kronenberg & Berkhout (1994). Strombids are predominantly tropical to subtropical. They are widespread in the Indo-West Pacific, where most genera and species occur. Other species are found in the eastern Pacific and western Atlantic (including the Caribbean Sea), and there is a single species on the African Atlantic coast. Most species occur in the intertidal and shallow subtidal zones, but a few live in deeper water.

Strombid shells (Fig. 15.121A–C) are heavy and reach a large size; the largest, *Lambis*, has a total length of almost 400 mm. They have a moderate to high spire and an enlarged last whorl. The outer surface of the shell varies from smooth to roughly nodulose, with the outer lip of adults of most genera flared outwards. The flaring is absent in juveniles, which sometimes closely resemble, and are easily mistaken for, cones (family Conidae). The anterior canal varies from short to long and typically has a U-shaped stromboidean notch near the anterior end. The paired eyes are on long eyestalks: the right eye has a shorter stalk which protrudes through the stromboidean notch, and the left eye peers out through the end of the anterior canal (Fig. 15.121D; Pl. 25.2). The aperture is usually long and narrow. There may be numerous ridges on the inner part of the aperture, and fewer ridges on the columella.

Bergh (1895) described the anatomy of several strombids and Little (1965c) investigated the anatomy of the Caribbean species, *Strombus gigas*. The unusual foot (Fig. 15.121D, E) is very narrow and muscular (see below) and bears a claw-like operculum (Fig. 15.121D, E, J). The mantle cavity contains a well-developed gill and long, narrow osphradium (Fig. 15.121E). The radula is rather short and consists of coarsely cuspidate central and lateral teeth, and finely cusped marginal teeth (Fig. 15.121F), a single central tooth flanked on each side by one lateral tooth and two marginal teeth. All species studied use their extensible snout and radula to feed on macroalgae and epiphytes (Robertson 1961a; Berg 1975). The salivary glands are long and thin, and the oesophagus lacks a gland. The stomach has a very long crystalline style. The nervous system is rather loose, with the oesophageal ganglia well separated from the pleural ganglia.

Five extant strombid genera are recognised. *Tibia*, with four species, is not recorded from Australia; it is found in deeper water than *Strombus* and *Lambis*, and is characterised by a very long anterior siphonal canal and a grooved posterior canal. *Rimella* is similar to *Tibia*, but has a shorter canal. Of the three recognised species of *Rimella*, only *R. cancellata* which has a central Indo-Pacific distribution is found in northern Western Australia. The single extant species of *Terebellum*, *T. terebellum*, has a long shell (Fig. 15.121C), streamlined for burrowing in the sand (Abbott, D.P. 1962; Jung & Abbott 1967), and looks more like an elongate *Oliva* than a strombid. This species has a central Indo-Pacific distribution and is found in tropical Australia from the Houtman Abrolhos in Western Australia to northern Queensland. The most diverse genus, *Strombus*, is distinguished by having solid, dull-surfaced shells, with the aperture notched, but otherwise simple. Of the 55 species of *Strombus* recognised by Walls in 1980, at least half are known from tropical Australia. Additional species

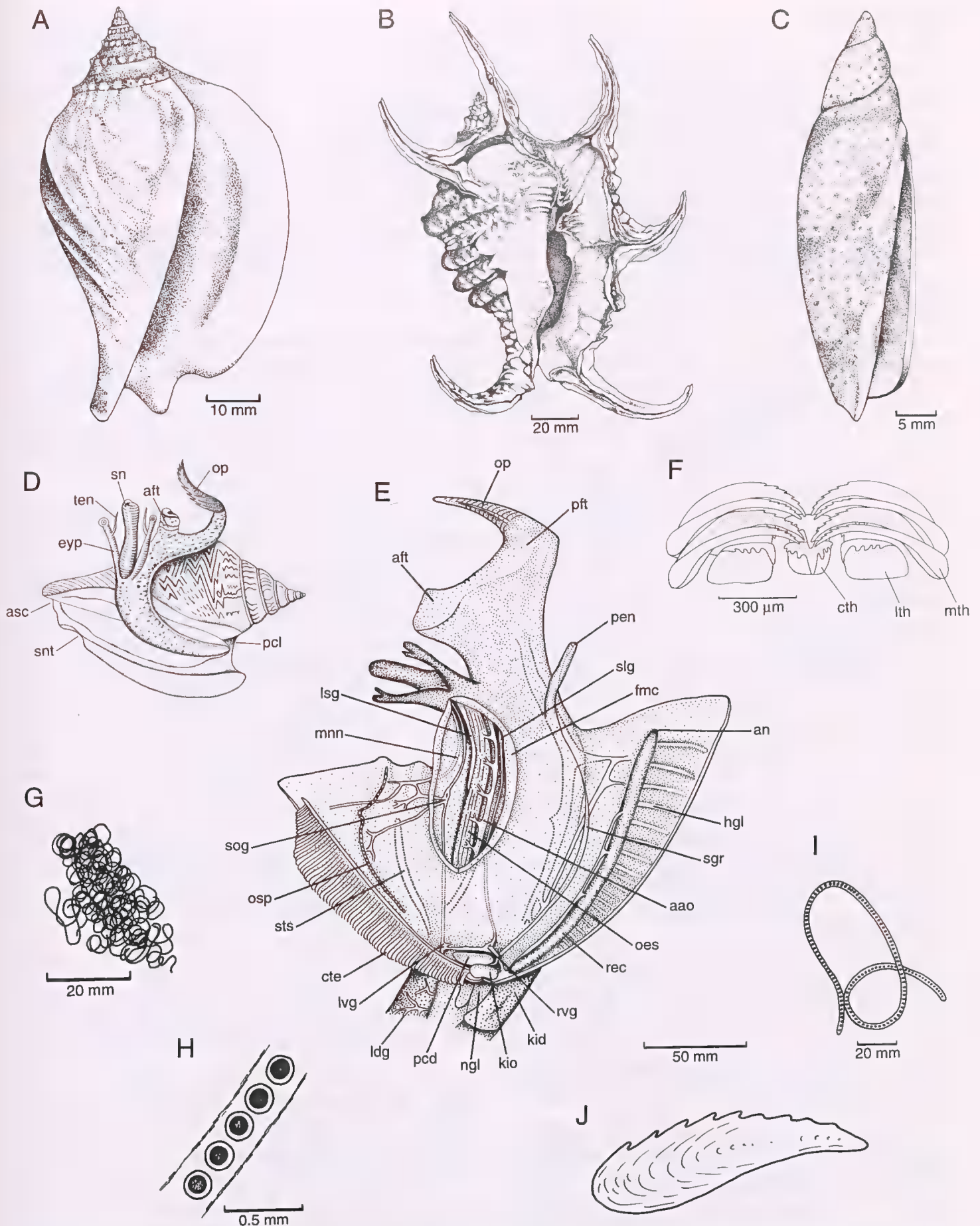


Figure 15.121 Family Strombidae. Shells, apertural view: A, *Strombus epidromis*; B, *Lambis chiragra*; C, *Terebellum terebellum*. D, *Strombus canarium*, external features of animal. E, male *Strombus gigas* with mantle cavity opened by a longitudinal cut between the ctenidium and hypobranchial gland; part of the floor of the mantle cavity is opened by a second longitudinal cut. F, *Strombus gibberulus gibbosus*, two of forty transverse rows of radular teeth. G–I, *Strombus maculatus*, egg mass and eggs: G, egg mass; H, egg strand; I, section of egg strand showing single row of eggs. J, *Strombus canarium*, operculum. aao, anterior aorta; aft, anterior portion of foot; an, anus; asc, anterior siphonal canal; cte, ctenidium; cth, central tooth; eyp, eye peduncle; fmc, floor of mantle cavity; hgl, hypobranchial gland; kid, kidney; kio, kidney opening; ldg, left anterior digestive gland; lsg, left salivary gland; lith, lateral tooth; lvg, left visceral ganglion; mnn, mantle nerve; mth, marginal tooth; ngl, nephridial gland; oes, oesophagus; op, operculum; osp, osphradium; pcd, pericardium; pcl, posterior canal; pen, penis; pft, posterior portion of foot; rec, rectum; rvg, right visceral ganglion; sgr, seminal groove; slg, suboesophageal ganglion; sn, snout and mouth; snt, siphonal notch; sog, supra-oesophageal ganglion; sts, style sac; ten, tentacle. (D, F–J, after Abbott, R.T. 1960; E, after Little 1965c) [A–C, G. Parker; D–J, A.J. Hill]

15. PROSOBRANCHS

have been recorded since, by Loch (1990) and Wilson (1993); Wilson illustrated most of the Australian species. A few species found in Australia extend into temperate waters, for example *Strombus mutabilis* which is widespread in the Indo-West Pacific, is found in south to central New South Wales on the east coast and to Cape Leeuwin on the west coast, and *S. campbelli* extends to northern New South Wales on the east coast. *Strombus* species are characteristically found on sand or slightly muddy bottoms in the intertidal or shallow subtidal zones. *Lambis* species, the spider or scorpion shells, have large shells with very long spiniform extensions of the flaring outer lip and are represented by nine Indo-West Pacific species, five of which also occur in Australia. *Lambis crocata*, *L. truncata*, *L. chiragra* and *L. lambis* (Pl. 25.3) are widespread across tropical Australia with *L. lambis* extending to southern Queensland; *L. scorpius* is found in northern Queensland. *Lambis chiragra* and *L. truncata* are common on intertidal coral reefs, but the other species live on sand.

Sexes are separate, with sexual dimorphism recorded in several species (Abbott, R.T. 1949, 1960, 1961, 1967), the males being significantly smaller than females. Pallial genital ducts are open and a genital groove runs to the anterior corner of the foot in females. There is a pallial sperm furrow in males; the end of the penis is widened and the margins are villous, with small spines in *Terebellum*. The animals may form dense mating aggregations during the spawning season (for example, see Randall 1964; Catterall & Poiner 1983; Stoner & Lally 1994). Berg (1975) described the mating behaviour of two Caribbean species of *Strombus*. After mating, females spend 12 to 24 hours depositing eggs in long, thin gelatinous strings (Pl. 25.1) that are woven back on themselves to form a complex mass (Fig. 15.121G–I). Females may spawn more than once in a season (Berg 1975). It is typical for the egg mass to contain 100 000 to 500 000 eggs that hatch into planktonic veligers in four to five days (Robertson 1959). After a planktonic life of two to three weeks the veligers settle to the bottom and metamorphose into juveniles. There is little information on the longevity of strombids, but Walls (1980) speculates that the larger species live for at least three years. Development and organogenesis of the Caribbean species, *Strombus gigas*, has been described in detail by D'Asaro (1965). Dispersion of juveniles has also been studied in Caribbean species (for example, Appeldoorn 1985; Stoner *et al.* 1988).

Another interesting feature of strombid biology is the method of locomotion, which was described in detail by Berg (1974, 1975). Most gastropods use muscular waves down the sole of the foot to move forward, usually aided by mucus secreted to reduce friction with the substratum. The strombid operculum is reduced in size, and is usually sickle-shaped with serrations on one side. The end of the operculum extends into a sharp point beyond the tip of the muscular foot. When the animal moves, the foot is fully extended and the operculum is jabbed into the bottom by contractions of the foot muscles. The animal is then pulled forward by the foot and the process is repeated (see Fig. 14.10A). If the shell is turned over the foot is extended and twisted until it makes contact with the substratum, then it is twisted sharply to throw the shell off the bottom (see Fig. 14.10B). The process is repeated until the strombid lands upright. The strong foot with the pointed operculum can also be used in defence (Randall 1964) or in an escape response (Field 1977).

Strombids are edible and fisheries have developed around several species that occur in very high densities. The largest of these fisheries is for the queen conch, *Strombus gigas*, which has been fished extensively in the Caribbean. The animal is regarded as a delicacy and commands substantial prices; in many areas populations have declined due to over fishing to levels where fishing is no longer economic. A considerable scientific literature has developed on the fishery and general biology of *Strombus gigas* (for example, Randall 1964; Hesse 1979; Appeldoorn 1985, 1988; Iversen, Rutherford, Bannerot & Jory 1987; Stoner, Lipcius, Marshall & Bardales 1988). Several strombid species are eaten in the Indo-West Pacific, particularly the spider shell *Lambis lambis*. In contrast to the Caribbean queen conch, there is

not a single scientific paper on the fishery biology of *Lambis* species. *Lambis lambis* is regarded as a delicacy by the Malays of the Australian territory of the Cocos (Keeling) Islands in the Indian Ocean, and it is fished extensively. The fishery is unregulated and it is not known whether conch fishing is restricted to sustainable levels. *Strombus luhuanus* was eaten by people on the south coast of Papua New Guinea: overfishing has occurred in very shallow water, but deeper populations have not been affected. *Strombus luhuanus* attains sexual maturity at two years of age and at a size of 35–60 mm (Asigau 1988; Poiner & Catterall 1988).

R.T. Abbott (1960, 1961) listed a number of species of *Strombus* and *Lambis* occurring in the fossil record of the Indo-Pacific, but no records were given for Australia. Darragh (1970) recorded *Strombus denticostatus* from the Australian Tertiary.

Family Struthiolariidae

Struthiolariids are distinguished from other stromboideans by the development of ciliary feeding and associated modifications of pallial organs, reduction of the buccal and oesophageal (crop absent) sections of the gut, and of the radula (Fig. 15.122C) and salivary glands. The nervous system is also specialised in the incorporation of the subintestinal ganglion in the nerve ring, and the young are brooded in a brood pouch (Morton, J.E. 1950).

Only three struthiolariid genera are extant: *Struthiolaria*, *Tylospira* and *Perrisodonta*. *Pellicaria* is sometimes considered to be a full genus but was recognised by Powell (1979) as a subgenus of *Struthiolaria*. The family only occurs in the colder waters of the Southern Hemisphere, with a single Recent Australian species (*Tylospira scutulata*), two in New Zealand (*Struthiolaria papulosa* and *Pellicaria vermis*; Neef 1970; Powell 1979), and also species at South Georgia and Kerguelen Island. The family has a long geological history extending back to the Upper Cretaceous of New Zealand and the Miocene of Australia. The New Zealand species were revised by Marwick (1924, 1950), Vella (1953) and Neef (1970), and Zinsmeister & Comacho (1980) have revised Antarctic struthiolariids. The Australian genus, *Tylospira*, was revised by Darragh (1991). There are nine fossil species ranging from Early Miocene to Late Pliocene and Pleistocene. *Tylospira scutulata* occurs from the intertidal zone to about 100 m off New South Wales. In the Australian Museum there is an isolated record of a collection from a depth of 1500 m, but the shell may have been washed to this depth after the animal died.

The shell of *Tylospira scutulata* is large, up to 60 mm high, heavy, with a high turreted spire, a pronounced shoulder, and a channelled suture (Fig. 15.122A). The upper whorls are more angular, with small nodules on the margin. The lower whorls are rounded, the surface smooth and glazed except for the axial growth lines. The aperture is oval, the columella broad, callused and white. The outer colour is a light brown with several spiral brown lines across the last whorl, fewer on the upper whorls, and brown axial lines. The operculum has a thickened outer chitinated rim, tapered and produced into a spine (Fig. 15.122B).

There have been no biological investigations of *Tylospira scutulata*, but J.E. Morton (1950, 1951a, 1956) investigated *Struthiolaria* and *Pellicaria* and J.E. Morton & Miller (1968) provided information on their natural history. In New Zealand, struthiolariids occur in intertidal or shallow subtidal zones where they lie buried 20–30 mm deep in fine sand. The animals can be found easily by locating a hump in the sand with two holes. These holes are for inhalant and exhalant water flow, and are made by the proboscis and lined with mucus to bind the sand together (Fig. 15.122D). A single pallial tentacle extends through the exhalant hole, maintaining contact with the surface. The animals are ciliary mucous feeders (Morton, J.E. 1951a). The inhalant water flows over the gills, and as it does so, suspended particles such as diatoms, dinoflagellates and detritus become trapped on the gill surface, become embedded in mucus and are moved by ciliary

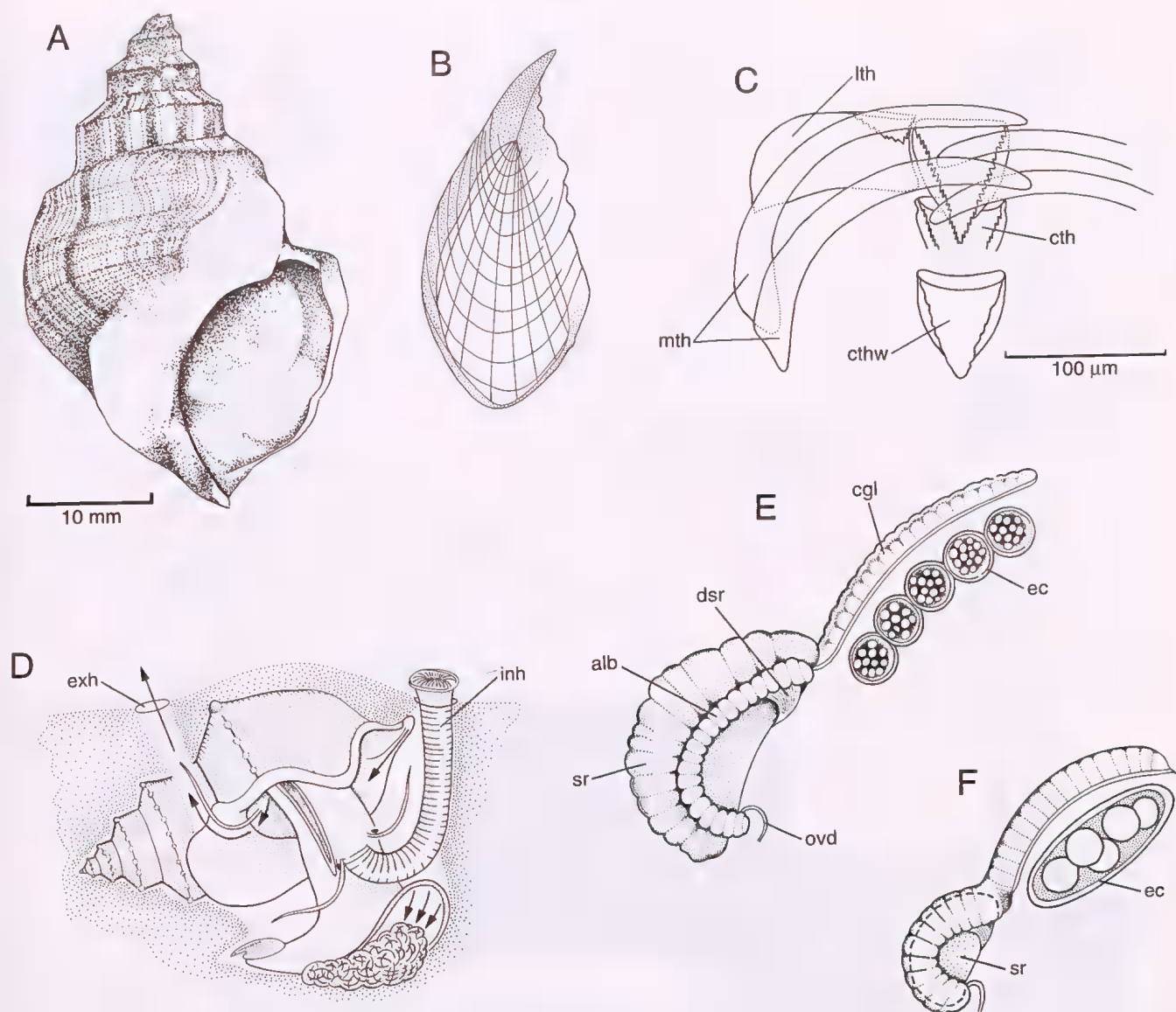


Figure 15.122 Family Struthiolariidae. A–C, *Tylospira scutulata*: A, shell, apertural view; B, operculum, diagrammatic view of inner surface – the thickened chitinous rim which is produced to form the spine is stippled; C, half a radula row of unworn teeth, and a central tooth from further forward, its cusp worn. D, *Struthiolaria papulosa*, animal buried below the surface, showing the mode of formation of the siphonal tubes. E, F, female genital ducts: E, *Struthiolaria papulosa* with portion of string of egg capsules, right lateral view; F, *Pelicaria vermis* with egg capsule, right lateral view. alb, albumen gland; cgl, capsule gland; cth, central tooth; cthw, central tooth, cusp worn; dsr, duct of seminal receptacle; ec, egg capsule; exh, exhalant siphonal aperture; inh, inhalant siphonal aperture; lth, lateral tooth; mth, marginal teeth; ovd, oviduct; sr, seminal receptacle. (B, C, after Morton, J.E. 1956; D, after Morton, J.E. 1951a; E, F, after Morton, J.E. 1950)

[A, G. Parker; B–F, A.J. Hill]

action to the edge of the gill. The mucous bound food is moved along a ciliary tract to the edge of the mantle cavity at the base of the right tentacle, where it is ingested with the aid of the radula.

The sexes are separate in struthiolariids. The genital ducts are primitive. Males have a simple prostate gland, and the ciliary sperm duct is open to the tip of the penis. Females also have an open ciliated genital furrow and an open capsule gland (Fig. 15.122E, F), and in all species have brood pouches in the mantle where young develop. In *Struthiolaria papulosa*, several hundred eggs develop to a four-lobed veliger stage before being released to a planktonic larval stage. In contrast, in *Pelicaria vermis*, less than a dozen young develop, and they remain in the female until being released as crawling juveniles (Morton, J.E. 1950).

The family has a long fossil history, extending back to the Late Cretaceous in New Zealand, the Eocene in Antarctica and the Oligocene in southern South America. In Australia, the group dates from the Early Miocene (Zinsmeister & Camacho 1980; Darragh 1991).

Superfamily VANIKOROIDEA

The Vanikoroidea, often referred to as the Hipponicoidea, is a rather small, but conchologically diverse superfamily of exclusively marine neotaenioglossan snails and limpets. The shells range from variously coiled snails (Vanikoridae) to cap-shaped sessile limpets with a shelly ventral plate (Hipponicidae). Species with planktotrophic development differ from members of the otherwise rather similar Capuloidea (Capulidae) in not having echinospira larvae, and from the Calyptraeidea in not being filter feeders. The shell aperture is simple, without an anterior canal.

As presently constituted, the Vanikoroidea may be paraphyletic. It is poorly known anatomically and no synapomorphic features have been identified as yet. The Fossaridae were included in this superfamily, but are now placed in the Cerithioidea (Ponder 1980a), as a subfamily of the Planaxidae (Houbrick 1990a). The families included are the Vanikoridae, Hipponicidae, and the Haloceratidae which is provisionally placed here for the first time.

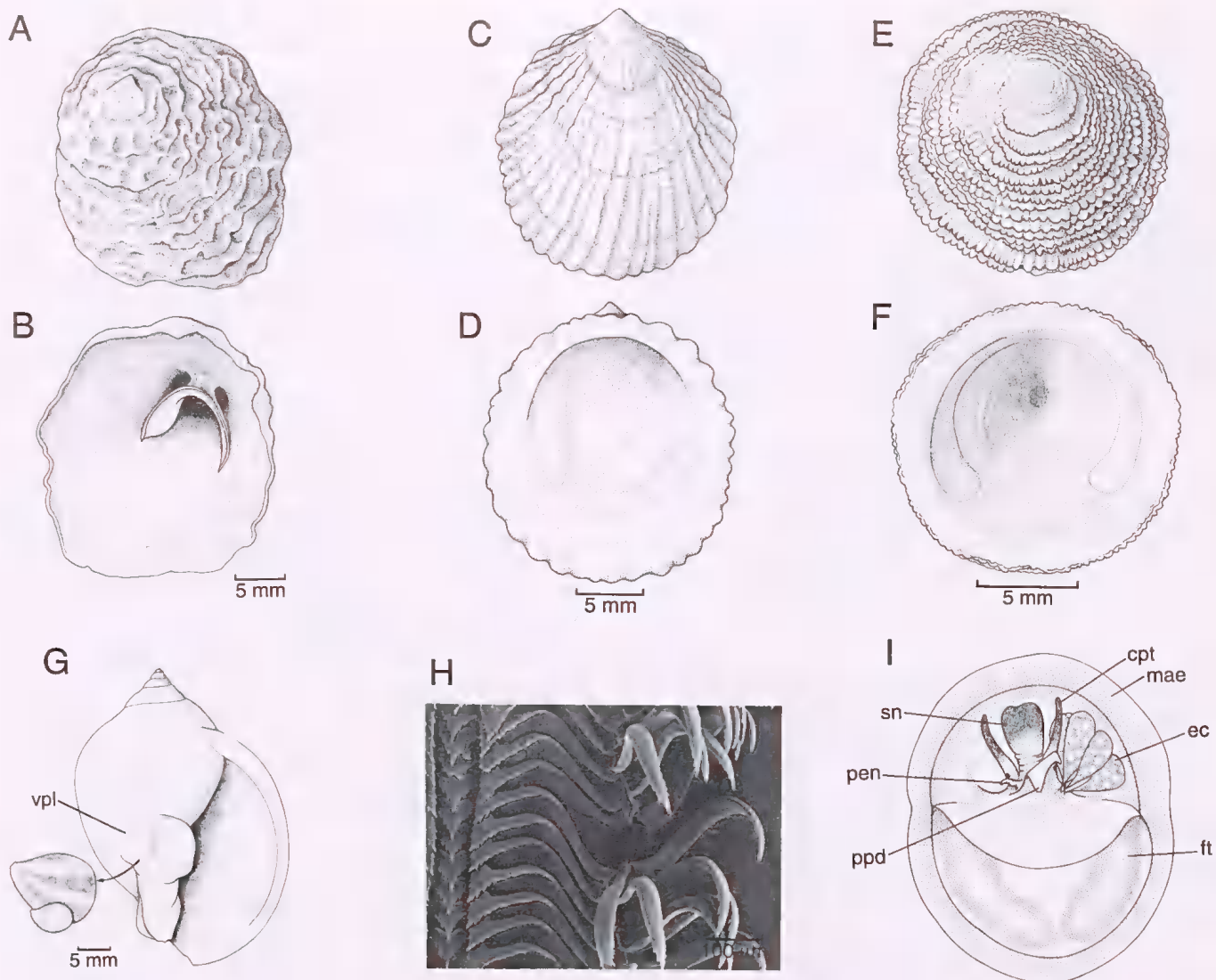


Figure 15.123 Family Hipponicidae. Shells, dorsal and ventral view: A, B, *Cheilea equestris*; C, D, *Sabia australis*; E, F, *Antisabia foliacea*. G, *Malluvium devotus* removed from *Phalium pyrum* showing the ventral plate attached to the 'host' shell; a smaller male is attached to the larger female *Malluvium*. H, half radular tooth rows of *Malluvium devotus*. I, female *Sabia australis*, ventral side, with the anterior foot membrane turned back to show the placement of the egg capsules. cpt, cephalic tentacle; ec, egg capsules; ft, foot; mae, mantle edge; pen, vestigial penis; ppd, propodium; sn, snout; vpl, ventral plate. (I, after Laws 1970)

[A–G, S. Weidland; H, W.F. Ponder; I, C. Eadie]

Family Hipponicidae

These marine limpets have small, cap-shaped shells and a ventral plate secreted by the foot (Fig. 15.123G). There is a horseshoe-shaped muscle scar, with an anterior opening both on the inner shell surface and the plate (Fig. 15.123D, F). There is no operculum on the thin disc-shaped foot. Feeding is effected by use of the extensible snout. Some species are gonochoristic (have separate sexes), others are protandrous hermaphrodites, often with the large females having one or several small males attached to the shell. Egg capsules are attached to the mobile anterior part of the foot (propodium) and thus larvae are brooded within the shell (Fig. 15.123I). *Sabia conica* has been reported to have possible photoreceptors in the mantle (Cernohorsky 1968).

The Hipponicidae, previously often known as Amaltheidae, have been recognised as a distinct family since the 1860s. There have been differing opinions on generic limits, some authors referring most species to *Hipponix*. Iredale (1937b) resolved the family name problem and recognised genera on differences in the protoconch, as did Morrison (1965). Cowan (1974) recognised fewer genera and used the genus *Hipponix* for some extant species. The current classification is by no means stable.

The shells (Fig. 15.123A–G) are less than 30 mm in diameter, and range from cap-shaped to patelliform. The protoconch is somewhat variable in shape, but is generally neritiform in species with lecithotrophic development. The aperture of the teleoconch is

subcircular to oval, with a simple peristome. The spire is posterior to the centre and curves posteriorly. Some species are smooth, others have coarse, irregular concentric striae or lamellae and/or radial ribs. The interior of the shell is smooth in most genera and has a horse-shoe-shaped shell muscle scar with its opening placed anteriorly. Species of *Cheilea* have an internal projection on the shell (Fig. 15.123B). Adults lack an operculum.

The cephalic tentacles (Fig. 15.123I) are long, with eyes at their outer bases, or sometimes lacking (Knudsen 1993). The foot has a small, bifid propodium and a disc-shaped mesopodium. The pedal epithelium typically secretes a shelly plate which is firmly cemented to the underlying substratum (Fig. 15.123G). The tip of the long snout is vertically cleft and has ventral lobes. In the mantle cavity there is a large ctenidium, a narrow, ridge-like osphradium and an extensive hypobranchial gland. The wide rectum acts as a storage area for faecal pellets (Knudsen 1991).

Hipponicids are sessile throughout all but their very early life. Some are 'commensal' on shells of other molluscs, sometimes situated near the exhalant siphon where they can feed on faecal pellets of the host, using the long, extendable snout (Fig. 15.123I; Risbec 1935; Knudsen 1991). Other species such as the North American *Antisabia cranioides*, and the almost identical Australian and Indo-West Pacific *A. foliacea* (Knudsen 1993), feed on organic detritus, pieces of algae, etc., by groping for food with their snout (Yonge 1953; Knudsen 1993) or catching suspended particles with the lobe-like ends of the snout (Yonge 1953).

The radula is of normal taenioglossate form with large multicuspidate central teeth, very broad lateral teeth and long, multicuspidate marginal teeth (Fig. 15.123H). There is a pair of simple salivary glands and no oesophageal gland. The stomach is large and typical of style-bearing gastropods (Yonge 1953). Anatomical accounts of members of the family were given by Fischer (1862), Risbec (1942) and Yonge (1953).

Some hipponicids in this family are known to be protandrous hermaphrodites. The male has a long, sometimes bifid penis. The female is larger and often one or several males are attached to the female's shell. Laws (1970) states that sexual development in '*Hipponix conicus*' (= *Sabia australis*) is affected by the proximity of other individuals. Females may have a rudimentary penis (Fig. 15.123I), a relict of the prior male phase, which may be very brief if the individual is solitary. Yonge (1953) suggested that sperm stored in the seminal receptacle in the male stage may be kept for self fertilisation in the subsequent female stage. The eggs are large and yolky and are laid in transparent, oval capsules. The egg capsules (Fig. 15.123I) are either retained in the mantle cavity or attached to the calcareous ventral plate by the epipodium. The few species examined brood their eggs, which develop directly into the crawling stage. Kay (1979) has reported possible planktonic larvae in one Hawaiian species but this is doubted by Knudsen (1993). However, Bandel (1993b) has recorded planktonic larvae which he identified as '*Hipponix conica*'. Females of *Antisabia erma* (Knudsen 1993) hold up to 15 capsules, each containing 30 to 50 embryos. Records of development attributed to *A. foliacea* suggest that it is a species complex (Knudsen 1993); both direct and planktotrophic development have been recorded.

Hipponicids are found from the lower intertidal zone to the deep waters of the continental slope, where species of *Malluvium* often are common and found living on other gastropod shells (Fig. 15.123G). Intertidal species may be attached in crevices and on the undersides of rocks (as in *Antisabia* species), or in tidal pools and fringing reefs attached to other shells, the host either alive (see Fig. 15.177E) or occupied by a hermit crab (as in *Sabia* species). *Sabia australis* shows site preference for the right and anterior shell margin of *Haliotis* (Laws 1970). The shells of *Sabia* species often take on the shape of the sculpture of the shell upon which they live (Savrujev 1985). Knudsen's (1991) studies have added biological information on this species.

As noted above, there is some disagreement on the generic classification of the Hipponicidae, especially concerning the use of the genus name *Hipponix*. The type of *Hipponix* is based on a fossil from the Eocene of France, and we follow Morrison (1965) in restricting the genus to a few fossil species not represented in Australia. In all, six genera are recognised in Australia: *Pilosabia* (one species), *Sabia* (Fig. 15.123C, D; two species), *Antisabia* (Fig. 15.123E, F; two species), *Malluvium* (Fig. 15.123G; two species), *Cheilea* (Fig. 15.123A, B; two species) and *Leptonotis*, which has been found recently in Western Australia – species in this latter genus live in the apertures of shells occupied by hermit crabs (Bouchet & Warén 1993). No genera are endemic to Australia. The genus *Amathina* was sometimes included in the Hipponicidae, but is now known to be pyramidelloidean (Ponder 1987).

The earliest undoubted fossil hipponicids are from the Late Cretaceous (Bandel 1993a), but Australian records date back only to the Pliocene (Ludbrook 1957).

Family Vanikoridae

These marine snails have globose, small to medium-sized shells. The last whorl is large and inflated in most species and sculpture typically consists of spiral and axial ribs, the axial sculpture often predominant. The foot is divided into a thin, mobile anterior propodium and a discoidal mesopodium that has a characteristic lateral lobe on each side (Fig. 15.124D).

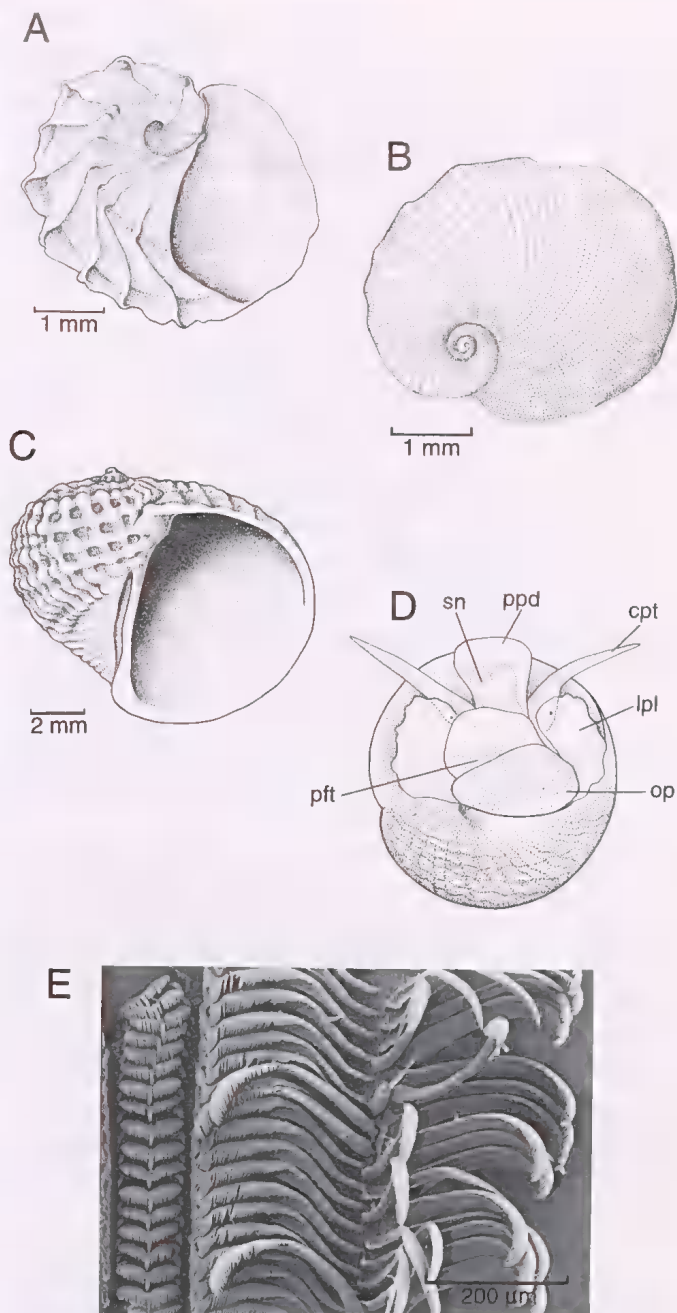


Figure 15.124 Family Vanikoridae. A, B, *Naricava angasi*, shell: A, ventral view; B, dorsal view. C, *Vanikoro cancellata*, shell, apertural view. D, head-foot of *Vanikoro cancellata*, ventral view; snout seen by transparency through propodium. E, half radular tooth rows of *Vanikoro cancellata*. cpt, cephalic tentacle; lpl, lateral pedal lobe; op, operculum; pft, dorsal side of posterior end of foot; ppd, propodium; sn, snout.

[A–D, S. Weidland; E, W.F. Ponder]

This family has been known under various names, largely due to the problem of the status of the name *Vanikoro*, which was introduced as a vernacular name. The family name has been variously known as Vanicoridae, Vanicoroidae, Vanikoroidae, Naricidae and Merriidae (Robertson 1962; Melville 1971) but the International Commission on Zoological Nomenclature has validated both *Vanikoro* and Vanikoridae. Smith (1908) last revised the Recent species of *Vanikoro*. Very little research has been done on the Vanikoridae since this review apart from Warén & Bouchet's (1988) revision of the north-eastern Atlantic species. The shells (Fig. 15.124A–C) are small to medium-sized (usually less than 20 mm wide), white, thin, fragile, globose with a small, conical, smooth or sculptured protoconch. The last whorl is usually large, rounded and inflated. Sculpture consists of axial ribs and, usually, spiral striae, the spirals sometimes dominant. The aperture is wide and oblique, with a concave, thin columellar margin and a broad, round, thin outer lip. An umbilicus may be present. The operculum is thin, corneous and paucispiral.

15. PROSOBRANCHS

The cephalic tentacles are well developed and flattened, with the eyes situated in swellings on the outer bases. The short snout is bilobed distally. The foot is distinctive in having a large lateral lobe on each side (epipodium of Boss 1982) which arises from the side of the large discoidal mesopodium (Fig. 15.124D). The propodium is mobile, thin and narrow. This pedal structure has been observed in all the genera mentioned below (W.F. Ponder personal observation) and is probably diagnostic for the family. Some genera are actively mobile (W.F. Ponder personal observation), but species of *Vanikoro* are sedentary and detached animals are apparently unable to re-attach themselves (Warén & Bouchet 1988).

Vanikorid anatomy has never been described adequately, but some information on *Vanikoro* has been published by Récluz (1945), Bouvier (1887), Bergh (1896) and Risbec (1955) and was summarised by Thiele (1929–1935) and Boss (1982).

The mantle cavity is spacious and contains a large ctenidium with triangular filaments and a long, narrow osphradium. Vanikorids are probably detritus feeders. The jaw consists of a pair of flattened plates. The radula is taenioglossate, short and wide, and has a broad central tooth with a pointed median cusp and numerous fine lateral cusps (Fig. 15.124E). The lateral teeth have many sharp cusps (see also Warén & Bouchet 1988). The stomach is very large and the salivary glands are short and thick.

Vanikorids are probably protandrous hermaphrodites. The male has a penis which is situated behind the right cephalic tentacle and has a closed penial duct. The pallial oviduct is also closed.

The green egg capsules of *Vanikoro helicoidea* are laid in a cluster, frequently piled on top of each other and partly overlapping, and are lens-shaped with a small, central, circular operculum. Each capsule contains many eggs and individual capsules tend to be at different stages of development (Cernohorsky 1978). Risbec (1931) has described the eggs and larvae of *Vanikoro cancellata*. *Vanikoro* species usually live in couples, the male being the smaller (Warén & Bouchet 1988).

Some species in this family live in shallow, tropical and subtropical seas beneath rocks associated with sand and weed, in the lower intertidal zone or shallow sublittoral. Many species are known from deeper water.

The taxonomy of this family is so poorly known that only a superficial indication of the faunal composition can be given. There are at least eight species of the globose-shelled *Vanikoro* in Australia, most of them wide-ranging tropical species. The dorso-ventrally flattened species assigned to *Naricava* (Fig. 15.124A, B), previously included in the Vitrinellidae or Adeorbidae, also belong here (W.F. Ponder personal observation on live animals). Several genera, including *Constantia* and *Nilsa* are tall-spined vanikorids, some of which live in deep water (Ponder 1985a; Warén & Bouchet 1988). Previously, on the basis of shell shape these species were referred to the Fossariidae or Rissoidae. The genus *Caledoniella* (on which the family name Caledoniellidae is based – see Rosewater 1969) was referred to the Vanikoridae by Ponder & Warén 1988. *Caledoniella* species are unusual in that they live attached to the undersides of stomatopod crustaceans; they may lack a radula (Rosewater 1969).

The Lyocylinae were included here as a subfamily by Ponder & Warén (1988). This very poorly known deep-water group has been found in Australian waters (A. Warén personal communication), but at present no information (other than details on shell characters) has been published.

The earliest vanikorid fossils, according to Wenz (1940), are possibly from the Upper Jurassic, but there are undoubted vanikorids from the Lower Cretaceous. Gougerot & Le Renard (1982) recorded a rich vanikorid fauna from the Eocene of the Paris Basin. Australian fossil species are not known, but some Recent species of *Vanikoro* are listed by Ladd (1972) from the Tertiary of the Marshall Islands and Fiji.

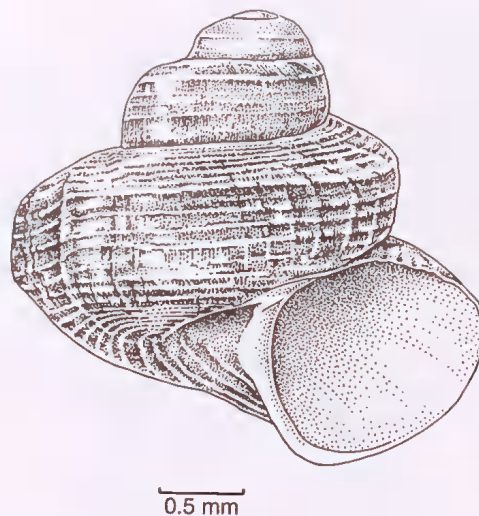


Figure 15.125 Family Haloceratidae. *Haloceras* sp., shell, apertural view. (After Warén & Bouchet 1991) [R. Plant]

Family Haloceratidae

This small family, named only recently (Warén & Bouchet 1991), is known from a few deep-water species. Haloceratids have a rather generalised anatomy (see below) and simple, mainly trochiform shells. Their inclusion in the Vanikoroidea is provisional. Warén & Bouchet (1991) indicated that this family is related to the Tonnoidea and Capulidae. It is excluded from the Capuloidea on the basis that it probably lacks an echinospira larva (Warén & Bouchet 1991) and from the Tonnoidea because it lacks most of the apomorphic features of that group.

Shells are disc-shaped to trochiform, of few teleoconch whorls and have spiral ribs (Fig. 15.125). The simple aperture lacks a siphonal canal and there is usually a broad, deep umbilicus. The periostracum is well developed and often fringed. The multispiral protoconch is predominantly spirally sculptured. There is a pair of moderately long cephalic tentacles with eyes at their bases. A short, pleurembolic proboscis is present. The foot has a lateral furrow along the edge, and anterior and posterior mucous glands. Within the mantle cavity there is a narrow ctenidium with finger-shaped filaments and a narrow, usually at least partly bipectinate, osphradium. Haloceratids are thought to be predators (Warén & Bouchet 1991).

Reproduction and life history are very poorly known, but the protoconch shows that most species have planktotrophic larvae, although one species is known to brood its young in a pallial pouch. There is also evidence to suggest that they are protandric hermaphrodites.

Several species of *Haloceras* are known from Australia and two species of the only other genus in the family, *Zygoceras*, are known from New Caledonia.

No fossil species are assigned to this family.

Superfamily CALYPTRAEOIDEA

The small marine superfamily Calyptraeoidae is similar to the Vanikoroidea and Capuloidea, but differs in that its members are filter feeders and have flattened shells with an internal shelf.

Under some classifications two or three families (Calyptraeidae, Capulidae, Trichotropidae; for example, Ponder & Warén 1988) have been referred to this superfamily, but here it is restricted to the Calyptraeidae alone, following the arguments of Warén & Bouchet (1991). The features of the single family remaining in this superfamily are thus those of the Calyptraeoidae. Unlike related groups, the Calyptraeidae have attracted considerable attention and a few species are well known anatomically (see for

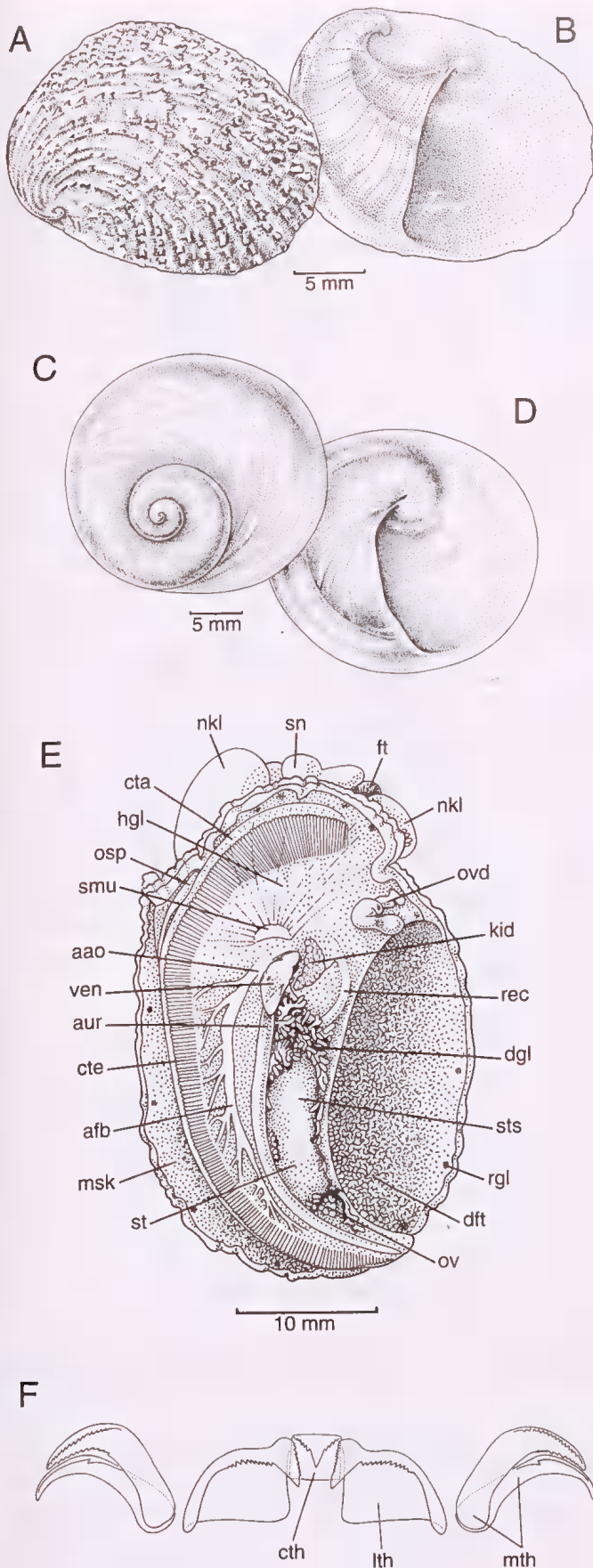


Figure 15.126 Family Calyptraeidae. A–D, shells, dorsal and ventral view: A, B, *Crepidula aculeata*; C, D, *Sigapatella calyptraeformis*. E, *Crepidula fornicata*, animal removed from shell, dorsal view. F, *Crepidula fornicata*, a single transverse row of radular teeth. aao, anterior aorta; afb, afferent branchial vessel; aur, auricle; cta, ctenidial axis; cte, ctenidium; cth, central tooth; dft, dorsal surface of foot; dgl, digestive gland; ft, foot; hgl, hypobranchial gland; kid, kidney; lth, lateral tooth; msk, mantle skirt; mth, marginal teeth; nkl, neck lobe; osp, osphradium; ov, ovary; ovd, pallial oviduct; rec, rectum; rgl, repugnatorial gland; smu, shell muscle; sn, snout; st, stomach; sts, style sac region of stomach; ven, ventricle. (E, after Fretter & Graham 1962; F, after Troschel (& Thiele) 1856–1893) [R. Plant]

example, Kleinstüber 1913; Giese 1915; Moritz 1938; Coe 1942; Yipp 1980; Hoagland 1986) and biologically (for example, Orton 1909, 1912; Gould 1919, 1952; Coe 1935, 1936; Walne 1956; Hendler & Franz 1971; Newell & Kofoed 1977; Ament 1978; Hoagland 1983, 1984a, 1984b; Pechenik & Lima 1984; Shenk & Karlson 1986; McGee & Targett 1989).

Family Calyptraeidae

Members of the Calyptraeidae are filter-feeding marine gastropods lacking an operculum, but having an expanded aperture and a foot adapted to a near-sedentary existence on hard substrata. Hoagland (1977) revised the genus *Crepidula*, including Australian species, however the other genera are in need of revision.

Calyptraeids have shells of length 5–50 mm, all with a widely open aperture giving the shell a limpet-like or abalone-like shape (Fig. 15.126A–D). Some are distinctly coiled with a low spire, others ear-shaped or patelliform, although all show at least some coiling at the apex. The columella is modified to form an internal partition (a cup, prong, or shelf; Fig. 15.126B, D) separating the foot from the viscera. This modification is most complete in the genus *Crepidula*, with its flat internal shelf (Fig. 15.126B). Genera are defined primarily by the shape of the partition. Shell sculpture is often absent, but various species have ribs, spines, costae or foliations on the shell. Shells vary from white to brown or purplish, often with darker rays or spots. Shell shape and colour vary within species.

Calyptraeids retain modified columellar muscles, and some have an additional shell muscle dorsal to the visceral mass. The highly muscular foot is disc-like and used as a sucker. Calyptraeids are capable of creeping, but most large species have difficulty re-attaching once removed forcibly. A pair of neck lobes (Figs 15.14, 15.126E) extend on each side as thin flaps. There is no operculum in the adult. The anterior portion of the shell is slightly raised for feeding and respiration. Modifications for filter-feeding include a large ctenidium (Fig. 15.126E) that arches across the very large, long mantle cavity, a mucus-secreting endostyle along the left side of the ctenidium, a food groove and a large hypobranchial gland (Fig. 15.9). A mono- or bipectinate osphradium lies on the pallial roof at the anterior edge of the mantle. The jaws are rudimentary and the buccal mass and radula small. The radula (Fig. 15.126F) has a wide lateral tooth and two narrow serrated marginals on each side of a finely cusped central tooth. The radular teeth are used to grasp the mucus-bound food strings produced as a result of ciliary feeding. Juveniles of some species use the radula for rasping food from the substratum before the gill is developed enough for filter-feeding (Hoagland unpublished data). The feeding process produces pseudofaeces. There are two long salivary glands and the anterior oesophagus lacks an oesophageal gland. Two digestive glands open into the stomach, which has a crystalline style containing cellulases.

All species are protandrous hermaphrodites. The penis of the male stage, which has an open ciliary sperm groove and may have a terminal filament, is resorbed during the sex change, although a stump may remain. Females have a glandular pallial oviduct and a cluster or row of seminal receptacles arranged characteristically for each species. A muscular anterior portion of the pallial oviduct is present in *Crepidula*, but is absent in *Calyptraea*.

Young are brooded in bunches of stalked sacs attached either to the foot or to the substratum under the female. The propodium and neck lappets form the brood chamber. The young are released either as planktonic veligers, pediveligers or as crawling young; the type of development is species-specific. Some species produce nurse eggs, and most show varying degrees of brood cannibalism (Hoagland 1986).

The young snails mature as males in their first season. Typically, a female can produce several broods per year, and can live for four to five years or longer. Fecundity increases with age and size; growth is indeterminate. Males attach to the shell of females,

15. PROSOBRANCHS

hence small size and mobility are advantageous to males. 'Stacking' of shells occurs in some species of *Crepidula*, with females at the base, grading up to males at the top (Coe 1936; Hoagland 1977). There is a definite age dependency of the sex change in some species, whereas sex change in taxa with planktonic larvae is often labile and depends upon external cues. It is assumed that pheromones plus hormones control sex change and gregarious behaviour. The sex ratio is biased towards males and becomes more so at high population densities.

Calyptraeids live subtidally in muddy bays or tidal pools, in or on empty shells or on any other hard substrata. Some species specialise in living on dead shells (often shared with a hermit crab) or on a particular species of living bivalve or gastropod. The flat species such as *Crepidula immersa* and *C. walshi* are found inside dead shells or under rocks, and are photonegative. Some spiny species such as *Crepidula aculeata* are frequently found, but cryptic, elements on rocky shores or coral reefs. Crabs are major predators, and pyramidellid snails are known to feed suctorially on the mantle tissue while the calyptraeid is filtering. Bird schistosomes have been found in some calyptraeids.

The Calyptraeidae are a worldwide family with five genera of certain affinity and one of uncertain status. The genera *Crepidula*, *Sigapatella* (which includes species previously classified in *Calyptraea*) and *Siphopatella*, but not *Crepidatella*, *Calyptraea* and *Crucibulum*, are found in Australia. Australian species are quite distinct from the largely endemic New Zealand calyptraeids, but Australia has a few species in common with the Pacific Islands (*Crepidula aculeata*) and the Indian Ocean (*Siphopatella walshi*). In northern and southern areas of Australia there is some overlap of eurythermal species. Most species are found on the New South Wales and southern coasts of Australia.

The Calyptraeidae first appear in the Upper Cretaceous (Wenz 1938–1944; Bandel 1993a). There is a rich fossil record for the family in New Zealand (doubtfully Upper Cretaceous, Palaeocene onwards), Japan (Miocene), Patagonia (Pleistocene) and the United States of America (Oligocene to Pleistocene) and Europe (Tertiary). Fossils have also been found in the Australian Tertiary (Darragh 1970).

Superfamily CAPULOIDEA

The Capuloidea are a small marine superfamily comprising a single family. Capulidae are characterised by having an echinospira larva, and a long pseudoproboscis (a dorsally split, tube-like extension of the mouth), and by being protandrous hermaphrodites and mainly filter feeders. Further details are given below under the family.

A characteristic feature of this grouping is the presence of an echinospira larva (Fretter & Graham 1962; Pilkington 1974, 1976). This type of larva is typified by a secondary larval shell or scaphoconch and also occurs in Lamellariidae, Velutiniidae, Triviidae and Eratoidae (Fretter & Graham 1962; Warén & Bouchet 1991), but not in the Calyptraeidae, a family with which capulids have traditionally been associated. Warén & Bouchet (1991) have advocated that the capulids and calyptraeids be separated and this course is followed here.

The earliest fossil records of capulids are from the Cretaceous (Wenz 1940).

Family Capulidae

The Capulidae (= Trichotropidae, Lippistidae) have tall-spined, coiled to limpet-shaped shells, usually with a thick, often bristly or fringed periostracum. An operculum is present in coiled capulids, but is absent in the adults of limpet-shaped taxa. An echinospira larva is present in species with planktotrophic development and the mouth is drawn into a proboscis-like structure with a dorsal longitudinal groove.

Capulids, as here envisaged, can be grouped into two sets that are usually considered to be two families – the limpet-shaped Capulidae, and the often tall-spined, coiled Trichotropidae – but these are combined following Ponder & Warén (1988) and Warén & Bouchet (1991).

Capulids range in shell form from coiled (Fig. 15.127A), as in *Trichotropis*, to limpet-shaped (Fig. 15.127B) as typified by *Capulus*, with some genera (for example, *Zelippistes*) being intermediate. They are small to medium-sized, some of the larger living species having shells reaching about 40 mm in maximum dimensions, although one fossil species attributed to this family (Hayami & Kanie 1980) has a shell up to 700 mm long! The shell surface is usually sculptured with spiral cords and, in some species, is cancellate. The aperture is simple or has a short anterior canal.

Capulids are characterised by their long 'pseudoproboscis' (Fig. 15.127D, E), an extension of the oral area. This structure is not tubular, but has a slit along its dorsal side. The mantle cavity contains a large monopectinate ctenidium (Fig. 15.127E) with elongate filaments. The osphradium (Fig. 15.127E) is simple, mono- or bipectinate. The pallial edge is smooth or tentaculate and with (*Capulus*) or without (*Trichotropis*) repugnatorial glands.

Capulids are mainly filter feeders (Yonge 1938, 1962), *Capulus* capturing the food, trapped by the gill and passed by ciliary action from the mantle cavity, on the extensible propodium. Some species of *Capulus* bore holes in the shells of the pectinids on which they live. These species are thought to feed on the pseudofaeces of the host rather than being truly parasitic (Orr 1962; Kosuge & Hayashi 1967; see also below). The pseudoproboscis is twisted to the right where it gathers the food string which is carried by cilia along the pseudoproboscis to the mouth. Jaws are very weak to absent and there is a pair of lobed salivary glands lying anterior to the nerve ring, their ducts very short. The radula is taenioglossate (Fig. 15.127F). Oesophageal glands are absent in *Capulus*, but present in *Trichotropis* (Graham 1954b). A crystalline style is present in *Capulus*, and present or absent in the large stomach in *Trichotropis* (Graham 1954b; Yonge 1962).

Capulids are protandric hermaphrodites (Graham 1954b; Thorson 1965), small individuals having a penis (Fig. 15.127D) with an open seminal groove, the penis being either lost (as in *Capulus*) or retained (as in the western American *Trichotropis cancellata*; Yonge 1962) in the female phase. The gonad simultaneously produces sperm and eggs in intermediate individuals. Females have an albumen and capsule gland and a posterior seminal receptacle (Giese 1915; Graham 1954b). There is no bursa copulatrix. A gono-pericardial duct is absent. Species of *Trichotropis* lay encapsulated eggs (Thorson 1931; Yonge 1962), but at least some species of *Capulus* brood eggs in an egg sac in the anterior mantle cavity (Fig. 15.28; Pl. 25.5; Orr 1962; Thorson 1965), larvae being released as planktotrophic veligers (Lebour 1937).

Capulids live mainly in the sublittoral zone and on the continental shelf. Species of *Capulus* are attached to the shells of other molluscs. Some species prefer pectinids and some of these, including the Queensland species, *Capulus sycophanta* (Fig. 15.127B, C; Garrard 1961) which commonly lives on *Amusium*, drill a hole through the shell of the host (Orr 1962; Kosuge & Hayashi 1967; Matsukuma 1978). Others may make a notch in the margin of the bivalve host (Habe 1967; Matsukuma 1978). Other species do not cause damage to the shell of the host (for example, the European *Capulus ungaricus*; Thorson 1965), although they are positioned at the edge of the aperture on gastropods and the shell margin on bivalves.

This is not a particularly diverse family, but according to Warén, Arnaud & Cantera (1986) about 40 generic names have been proposed for 'trichotropids' alone. These authors note that separation of genera is difficult. The group is in great need of taxonomic revision, there never having been a critical review of the genera or the Australian species. Species of the turbinat genus *Torellia* (see Warén *et al.* 1986) are named from Europe,

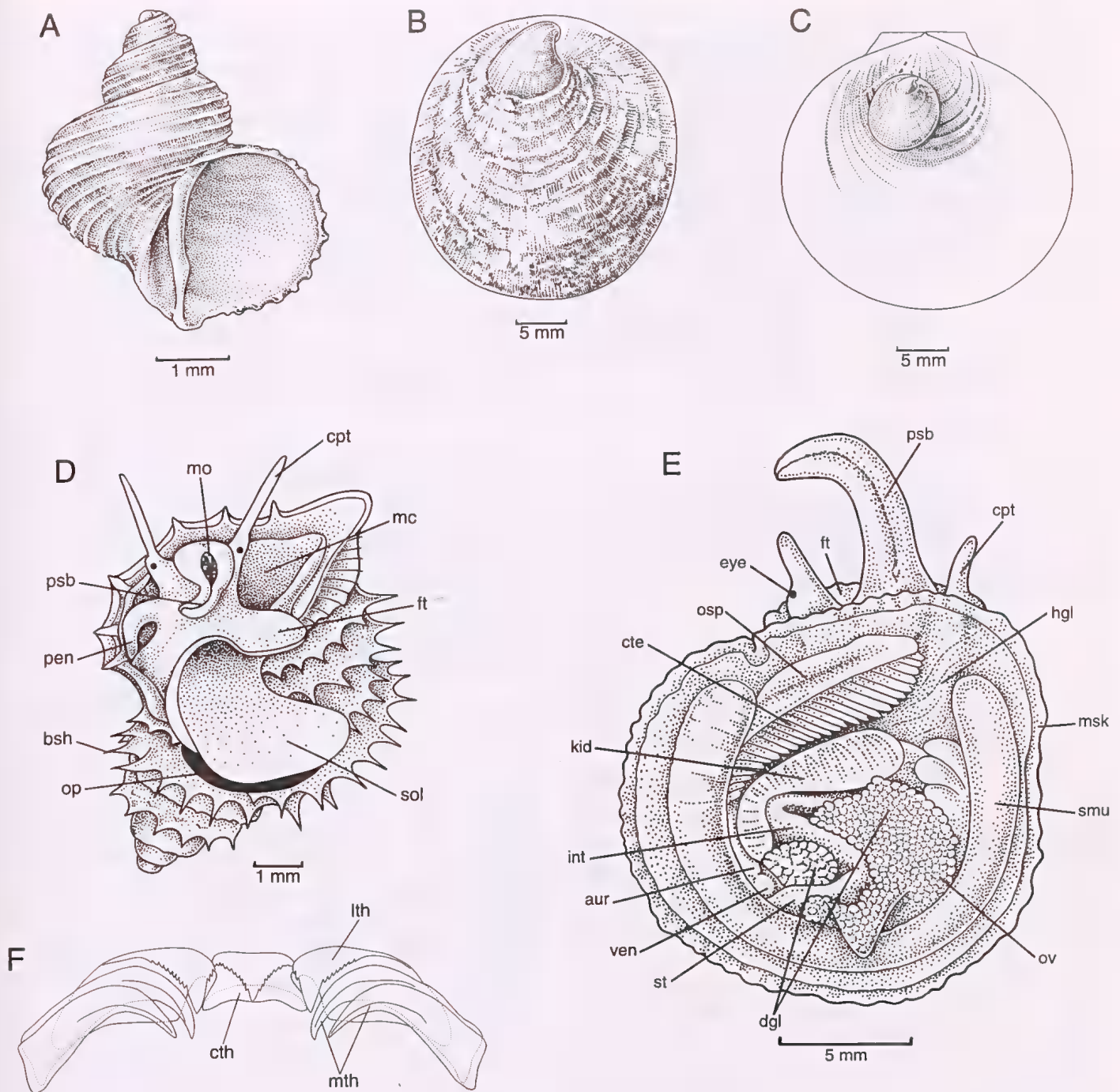


Figure 15.127 Family Capulidae. A, *Sirius badius*, shell, apertural view. B, *Capulus sycophanta*, shell, dorsal view. C, *Capulus sycophanta* living on a pectinid shell. D, *Trichotropis borealis*, male, ventral view. E, *Capulus ungaricus*, animal removed from shell, dorsal view. F, *Capulus ungaricus*, single row of radular teeth. aur, auricle; bsh, bristles on shell; cpt, cephalic tentacle; cte, ctenidium; cth, central tooth; dgl, digestive gland; eye, eye; ft, foot; hgl, hypobranchial gland; int, intestine; kid, kidney; lth, lateral tooth; mc, mantle cavity; mo, mouth; msk, mantle skirt; mth, marginal teeth; op, operculum; osp, osphradium; ov, ovary; pen, penis; psb, pseudoproboscis formed from ventral lip; smu, shell muscle; sol, sole of foot; st, stomach; ven, ventricle. (D, E, after Fretter & Graham 1962; F, after Troschel (& Thiele) 1856–1893) [R. Plant]

the Antarctic and Subantarctic and an unnamed species is known from deep water in the Tasman Sea (A. Warén personal communication). The higher-spired *Trichotropis* is found in the Northern Hemisphere and most of the similar-shaped species in Australia are referred to *Sirius* (Fig. 15.127A). The loosely coiled species of *Zelippistes* and *Separitista* are found, respectively, in New Zealand and Australia, but like most capulids in Australia these are rare.

Several Australian Tertiary species attributed to *Cerithioderma* have been described from the Lower Tertiary (see Darragh 1970) and other genera in the family are found throughout the Tertiary.

The parasitic limpet *Thyca* has been included in this family in the past, but is actually a member of the Eulimidae (Warén 1983), and *Amathina*, also often included here, is a member of the Pyramidelloidea (Ponder 1987).

Superfamily XENOPHOROIDEA

Members of the superfamily Xenophoroidea are characterised by their habit of accreting objects on their large tent-shaped shells. Their narrow, elongate foot is capable of 'stromboidean' motion, a feature shared with the Stromboidea. The head bears a long snout and long cephalic tentacles. The wide ctenidia are used only in cleansing, and in this they differ from the Calyptraeidea, a filter-feeding group to which they were thought to be allied (Morton, J.E. 1958). All three superfamilies have a long, narrow osphradium which runs the length of the ctenidium, a character which is probably plesiomorphic in caenogastropods. Xenophoroideans have an operculum and are gonochoristic, features not shared with calyptraeideans which lack an operculum and are protandrous hermaphrodites. They may be most closely allied to the Stromboidea, as both have a crystalline style, lack

15. PROSOBRANCHS

oesophageal glands and have a similar foot and locomotion. The Xenophoroidea differs from the Stromboidea principally in shell shape, the lack of pedunculate eyes and anterior inhalant siphon, in details of the radular morphology and in the structure of the female reproductive system. The pallial section of the female duct in stromboideans is open or partly open but is closed in Xenophoridae. The xenophorid female system is also peculiar in that it has an anterior oviduct gland separated from the rest of the pallial oviduct, a large posterior sperm sac of uncertain homology and a separate anterior sperm sac (Ponder 1983c).

The superfamily contains only one extant family Xenophoridae, consequently, further details are given under the family.

Although undoubted xenophorid fossils date only from the Cretaceous, representatives of one or two older, extinct families with similar shells were thought possibly to be related (Ponder 1983c), although this is unlikely (Bandel 1993a).

Family Xenophoridae

Xenophorids are medium to large (shells usually less than 100 mm in diameter) marine snails. They are commonly known as 'carrier shells', due to their habit of cementing debris to the dorsal surface of their shells. The foot is narrow and elongate, the salivary glands are unusually large, the large stomach has a crystalline style and the mid-oesophagus lacks oesophageal glands but is expanded to form a crop.

J.E. Morton (1958) studied the habits and relationships of the Xenophoridae. Linsley & Yochelson (1973) have discussed the habits of the family, comparing members to some accreting Middle and late Devonian eumophalids. Ponder (1983c) described aspects of their anatomy, reviewed the Recent species on a worldwide basis and (in an appendix with J. Cooper) listed the fossil species.

Xenophorid shells (Fig. 15.128A–D) are broadly conical with a depressed spire and a flat to concave base rimmed by a simple to digitate, flanged periphery that sharply separates the spire from the base. The protoconch (Fig. 15.128K) is usually multispiral and conical, rarely paucispiral. The dorsal surface of the teleoconch usually has foreign material cemented to it in spiral series. The horny operculum (Fig. 15.128E–G) has a lateral nucleus, simple growth lamellae and sometimes conspicuous, radial striae or hollow, radial ribs (Ponder 1983c).

The head has a long snout and the cephalic tentacles are long with the eyes on swellings near their outer bases. The narrow foot has anterior pedal glands and is laterally compressed, the sole being much reduced. Locomotion is somewhat similar to that seen in Strombidae, the side of the foot being placed against the substratum and the shell lifted by the extension of the muscular column. The shell is then thrust forwards for about half its diameter and then falls forward (Linsley & Yochelson 1973).

The edge of the mantle sometimes has a row of very short tentacles, and on the right a glandular swelling (Fig. 15.128I) which probably produces secretions that are utilised in the binding of faecal waste. The ctenidium (Fig. 15.128I) is large and used in respiration and cleansing (Morton, J.E. 1958) and, although composed of numerous long filaments, is not used in filter feeding. The osphradium (Fig. 15.128I) is long and thread-like, and a well-developed hypobranchial gland (Fig. 15.128I) lies between the ctenidium and the rectum.

Gut contents of several species of *Xenophora* examined by Ponder (1983c) contained miscellaneous detritus and a high silt content; *X. (Onustus) exuta* appears to feed exclusively on Foraminifera. The American *X. conchyliophora* feeds selectively on fine filamentous algae (Berg 1975). During feeding in that species the snout is extended and food is collected from the substratum beneath the shell (Shank 1969). The radula (Fig. 15.128H) is short, small and taenioglossate. The central teeth are large and have few cusps, the medium cusp being large. The lateral teeth are short and have only one prominent cusp and a long simple cutting edge. The marginal teeth are weakly dentate and curved.

Faecal material is stored in the rectum (Fig. 15.128I) and discharged periodically (Ponder 1983c). Shank (1969) observed that *X. conchyliophora* buried its faeces in a hole made in the substratum by the snout which was then used to close the hole.

The kidney is small and heavily plicate internally, lying at the posterior end of the mantle cavity. The circumoesophageal ganglia (Bouvier 1887) are not concentrated. The pedal ganglia are separated by long commissures. The buccal, visceral and oesophageal ganglia are widely separated from the circumoesophageal ring, although the cerebral and pleural ganglia are in contact. The statocysts each contain a single statolith.

The larvae of Xenophoridae are unknown, but the protoconch morphology suggests that nearly all species are planktotrophic (Ponder 1983c). Dispersal by planktonic larvae probably accounts for the wide geographic range of some species. There is, however, a southern Australian species of *Xenophora*, *X. flindersi*, which has a paucispiral protoconch, indicative of direct development.

Sexes are separate, males having a large penis and lacking a large pallial prostate gland. The penes of some species have accessory glandular or non-glandular structures and the seminal groove often terminates on a papilla. Females have the vaginal opening on the posterior part of the mantle cavity and this opens to an 'egg groove' (Fig. 15.128J) which terminates on the right side of the foot. Fertilisation probably takes place at the posterior part of the vaginal tube. The oviduct gland lies rather far back in the pallial cavity and has a closed, blind anterior section which is continuous with a visceral continuation of the gland. Usually, there is one anterior and one to several posterior sperm sacs (Ponder 1983c).

Xenophorids are found on the continental shelves and slopes of most tropical and temperate regions but little is known of their biology and ecology. They are particularly notable because of their habit of fixing foreign objects (sand grains, shells, pebbles, etc.) to the dorsal surface of their shells. Objects are manoeuvred into position by the snout and tentacle bases in the American *X. conchyliophora* (Shank 1969), or by the propodium in the New Zealand species, *X. neozelanica* (Linsley & Yochelson 1973). The shell is raised and lowered by the trunk and the foot (in *X. conchyliophora*) or by the snout (in *X. neozelanica*). When the object and the shell are positioned (in *X. conchyliophora*) the shell surface is cleaned and the object is cemented in place by secretions from the mantle edge, gaps being filled in with sand and small bits of debris.

Little is known of the behaviour of xenophorids, but observations suggest that they have evolved a suite of behaviours to enable them to escape detection by predators. Strategies include their feeding posture, method of locomotion, the habit of burying the faeces and the attachment of debris for camouflage (St Jean 1972). Implanted material overhangs the periphery and provides a frill or wide peripheral flange that facilitates movement and feeding. Species that accrete few objects on their shells generally live on soft bottoms in relatively deep water where large attachments to the shell would make them conspicuous.

Ponder (1983c) recognised only one extant genus, *Xenophora*, in this family, the 22 extant species being divided into three subgenera: *Stellaria* (five species); *Onustus* (four species); and *Xenophora sensu stricto* (13 species). The subgenera are separated largely on differences in shell characters. Species included in *Onustus* have the ventral side of the peripheral flange porcellaneous; those in *Stellaria* have a wide peripheral flange which may be digitate or broken up into spines, whereas species of *Xenophora sensu stricto* have a simple, narrow peripheral flange. There is only one species of *Stellaria* in northern Australia, *X. (S.) gigantea*, which also occurs in the Indian Ocean and central Indo-Pacific. Two species of *Onustus* occur in Australian waters, *X. (O.) indica* and *X. (O.) exuta*; both are wide-ranging in the central Indo-Pacific. Extant *Xenophora sensu stricto* in Australia are *X. (X.) cerea*, *X. (X.) solarioides*, *X. (X.) mekranensis kono*i and *X. (X.) pallidula* which are wide-ranging, mainly tropical species, the latter attaching large, often elongate, shells in a radial

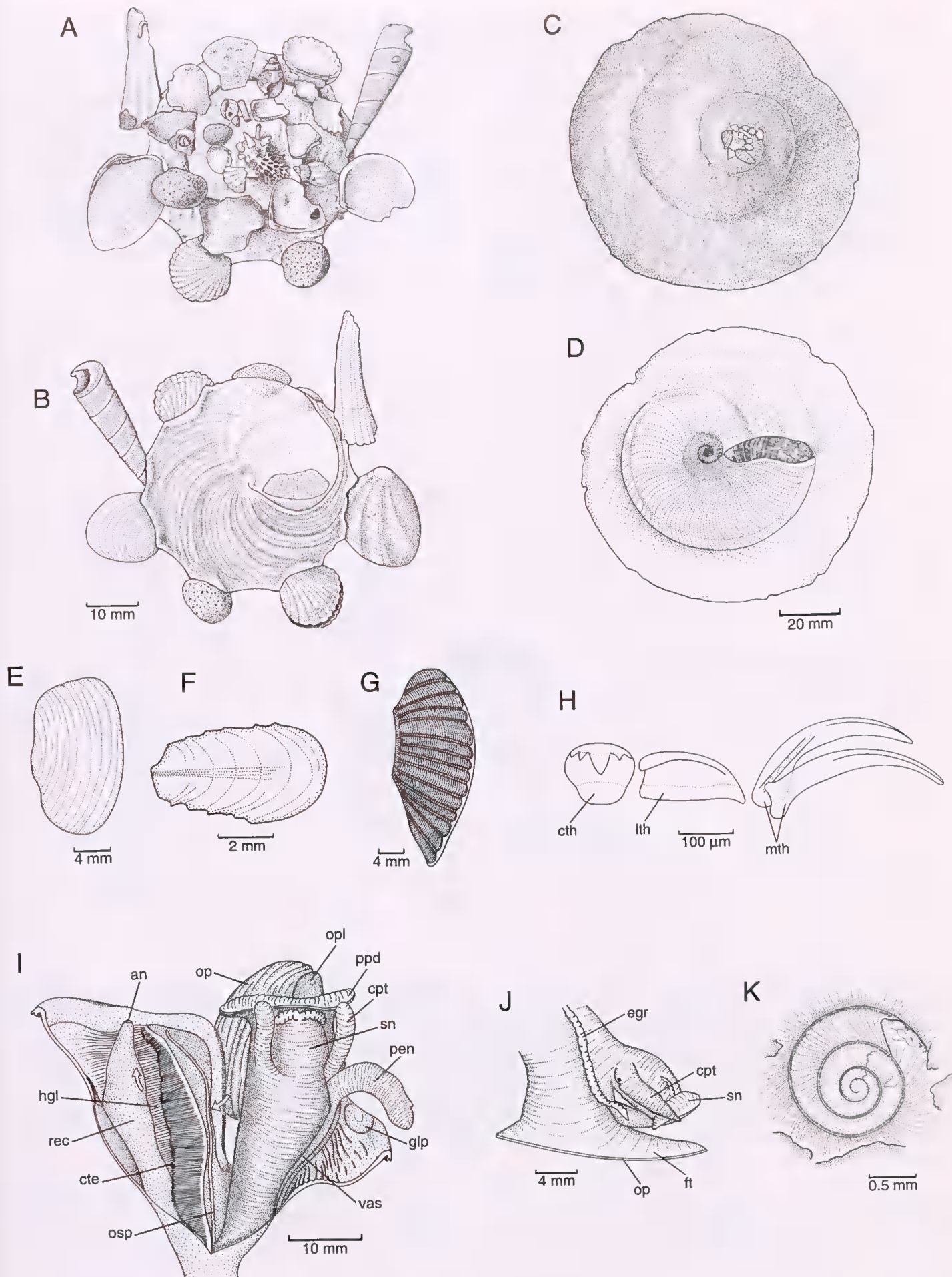


Figure 15.128 Family Xenophoridae. A–D, shells, dorsal and ventral views: A, B, *Xenophora (Xenophora) peroniana*, from New South Wales; C, D, *Xenophora (Onustus) indica*, from Queensland. E–G, opercula: E, *Xenophora (Xenophora) pallidula*; F, *Xenophora (Xenophora) flindersi flindersi*; G, *Xenophora (Onustus) indica*. H, *Xenophora (Xenophora) solarioides*, half a transverse row of radular teeth. I, *Xenophora (Xenophora) neozelanica*, male with pallial cavity opened, dorsal view. J, head-foot of female *Xenophora (Onustus) indica*, lateral view. K, protoconch of *Xenophora (Xenophora) neozelanica*. an, anus; cpt, cephalic tentacle; cte, ctenidium; cth, central tooth; egr, egg groove; ft, foot; glp, glandular pad; hgl, hypobranchial gland; lth, lateral tooth; mth, marginal teeth; op, operculum; opl, opercular lobe; osp, osphradium; pen, penis; ppd, propodium; rec, rectum; sn, snout; vas, vas deferens. (E–K, after Ponder 1983c) [A–D, S. Weidland; E–K, C. Eadie]

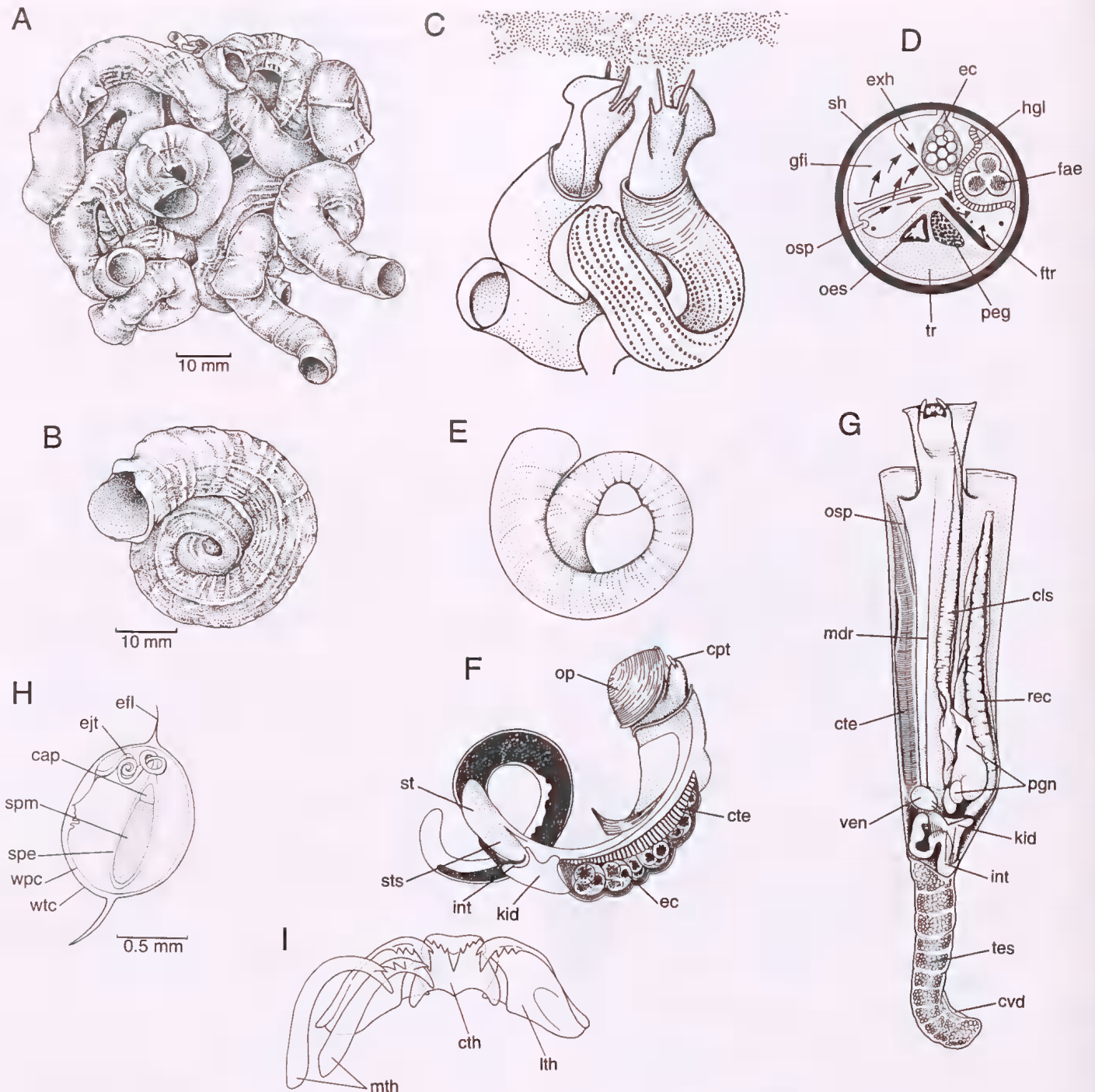


Figure 15.129 Family Vermetidae. A, *Serpularbis siphon*, many irregularly coiled shells forming a colony. B, *Serpularbis siphon*, shell of a solitary animal. C, *Aletes squamigerus*, semidiagrammatic view with portion of communal mucous sheet. D, *Serpularbis* sp., diagrammatic transverse section through the pallial cavity showing the position of the principal ciliary currents. E, *Dendropoma lamellosa*, nucleus attached to earlier portion of adult shell. F, *Dendropoma irregulare*, female removed from shell, mantle cavity opened to show the position of the egg capsules. G, *Serpularbis squamigerus*, male with mantle cavity opened along the dorsal mid-line to show the pallial structures. H, *Petaloconchus montereyensis*, spermatophore structure. I, *Dendropoma lamellosa*, single transverse row of radular teeth with the right marginals omitted. cap, cap between sperm mass and ejaculatory tube; cls, ciliated strip; cpt, cephalic tentacle; cte, ctenidium; cth, central tooth; cvd, coelomic vas deferens; ec, egg capsules; efl, end filament; ejt, ejaculatory tube; exh, exhalant chamber of pallial cavity; fae, faecal pellets in rectum; ftr, food tract; gfi, gill filament with tract of lateral cilia indicated; hgl, hypobranchial gland; int, intestine; kid, kidney; lith, lateral tooth; mdr, mid-dorsal ridge; mth, marginal teeth; oes, oesophagus; op, operculum; osp, osphradium; peg, pedal gland; pgn, pallial gonoduct; rec, rectum; sh, shell; spe, spheres in ejaculatory tube; spm, sperm mass; st, stomach; sts, style sac; tes, testis; tr, muscular region of trunk; ven, ventricle; wpc, wall of primary capsule; wtc, wall of tertiary capsule. (C, D, after Morton, J.E. 1955a; E, I, after Morton, J.E. 1951d; F, after Morton, J.E. 1965; G, H, after Hadfield & Hopper 1980) [A, B, R. Plant; C–I, A.J. Hill]

fashion, and being found in deep water in eastern and north-western Australia. *Xenophora* (*X.*) *peroniana peroniana* and *X. (X.) flindersi* are endemic to the east coast and south coasts respectively.

The earliest fossil species of *Xenophora* are found in the Cretaceous and are rather similar to *X. conchyliophora* or *X. peroniana* in having a spire of medium height, a simple base and a closed or narrowly open umbilicus. The genus diversified during the Palaeogene giving rise to the species existing today. Xenophorids are possibly allied to a Jurassic genus, *Jurassiphorus*

(Ponder 1983c). The earliest Australian fossil is a species of *Xenophora* from the Upper Cretaceous of northern Western Australia. By the Eocene the Xenophoridae were well established in the Tethys Sea and were diverse in Australia by the Miocene.

Superfamily VERMETOIDEA

The superfamily Vermetoidea comprises the single family, Vermetidae. Vermetids are sessile gastropods that have tubular, irregularly uncoiled shells cemented to a hard substratum such as

coral, rocks, jetty piles and other shells. They are often mistaken for tube worms and in some locations certain species may form significant bands on the shoreline. The characteristic features of vermetoideans are the uncoiled shell, lack of any apertural canal, simple to domed, spiral operculum (very reduced in *Vermetus* and lost in *Dendropoma*), reduction in the size of the foot, a long columellar muscle, and the presence of an enlarged pedal mucous gland.

Vermetids are unique in producing pelagic spermatophores. Sexes are separate, and males are aphyllous as in cerithioideans. The eggs are brooded either freely in the mantle cavity or attached to the inner shell wall and embryos are released at the crawling stage.

Family Vermetidae

Adult vermetids have a tubular shell, which is either regularly or irregularly coiled, and is permanently cemented to a hard substratum (Fig. 15.129A–C, E). They lack the anterior apertural canal found in most cerithioideans. The operculum, if present, is multispiral or paucispiral and circular with a central nucleus (Fig. 15.129F); its morphology is a useful aid in distinguishing genera. Larval shells have two to four whorls (Fig. 15.129E). Correlated with a sessile habitat, the foot is reduced. Statocysts are absent.

The shells closely resemble the tubes of some serpulid polychaetes. Several of the genera originally described as vermetids have subsequently been shown to be serpulids. These include such well-known genera as *Serpula*, *Spirorbis*, and *Spiroglyphus* (Keen 1961).

The position of the family Vermetidae has been of considerable debate in recent years. The family has been placed traditionally in the Cerithioidea, but J.E. Morton (1951b, 1951c, 1951d, 1955a) showed that it is unrelated to other cerithioidean groups (such as Siliquariidae and Turritellidae) that also have uncoiled shells. Houbick (1988) included the Vermetidae in his review of the phylogeny of the Cerithioidea, but although he showed that the family differs markedly from other cerithioideans in his phylogeny, he included it within the superfamily. Vermetids superficially resemble the filter-feeding Turritellidae in having a simple shell aperture, a food groove on the floor of the mantle cavity, and a brood pouch in the mantle cavity (Morton, J.E. 1955a, 1965; Houbick 1988). However, Healy (1988a, 1988b) showed that they differ from the Cerithioidea in sperm ultrastructure. He suggested that the group has closer affinities with the superfamilies Stromboidea, Calyptraeidea, Vanikoroidea, and Xenophoroidea. Ponder & Warén (1988) placed the Vermetidae in its own superfamily, Vermetoidea, which they located between the Xenophoroidea and the Cypraeoidea.

After a short crawling phase, the metamorphosing larva cements its shell by the apex to a hard substratum and begins to grow. At this stage some internal septa are present. Shell growth commences at a right angle to the protoconch whorls. The head has short cephalic tentacles with minute eyes at their outer bases (Fig. 15.129C, F, G). The foot is highly specialised, and has two tentacles arising from the anterior edges and a very large pedal gland; the mesopodium is reduced to a small sole. The mantle edge is smooth, in contrast to that of many cerithioideans, in which papillae are often present. The pallial cavity contains a long ctenidium with triangular leaflets, a broad hypobranchial gland, a ciliated food tract on the floor on the right side, and a long, narrow osphradium (Fig. 15.129D). The columellar muscle is long and strap-like, allowing the animal to withdraw deeply into the shell. This feature is shared with *Campanile* species (Campaniloidea). The buccal region is equipped with a pair of jaws, a small odontophore and tiny salivary glands. The radula teeth, with the marginals slender, are illustrated in Figure 15.129I. The oesophagus is simple and the stomach contains a crystalline style. The intestine is narrow and coiled, the rectum broad and packed with faecal pellets (Fig. 15.129G). Some vermetid species have a specialised method of feeding using a mucous net secreted by a

large pedal gland (Fig. 15.129C). Structural changes that reflect their mode of feeding include an enlarged pedal mucous gland and the loss of the oesophageal gland. Sexes are separate; females brood eggs in capsules retained in the mantle cavity. The capsules are attached to the inner surface of the shell along a deep slit in the roof of the mantle cavity. The female pallial genital duct is open along most of its length and there is a posterior seminal receptacle.

Our understanding of vermetid systematics was greatly improved by Keen's (1961) revision of the family. Keen recognised five genera, *Tripsycha*, *Dendropoma*, *Vermetus*, *Petalconchus*, and *Serpulorbis*, based on an analysis of coiling patterns, and features of the shell apex and operculum. With the exception of *Serpulorbis*, all of these genera have an operculum. J.E. Morton (1965), building on Keen's work, and his own earlier work on New Zealand species (Morton, J.E. 1951b, 1951d) reviewed vermetid anatomy and biology. In a subsequent examination of vermetids of the Hawaiian Islands, Hadfield, Kay, Gillette & Lloyd (1972) described several new species, finding that all fitted within the generic limits defined by Keen (1961). They listed the key characteristics of the four genera found in Hawaii as follows: *Dendropoma* has an entrenching shell and an elaborate operculum that fills the aperture of the tube; *Petalconchus* has an internal lamella and a small, concave operculum; *Serpulorbis* has a large, extensible, brightly coloured foot; and *Vermetus*, resembles *Petalconchus* with its small operculum, but lacks internal shell lamellae. These four genera are found in Australia but the Australian members of the family have never been revised, with the exception of the species from Rottnest Island, Western Australia (Hughes, R.N. 1993). Barash & Zenziper (1985) reviewed the structural and biological adaptations of some vermetids and R.N. Hughes & Lewis (1974) and R.N. Hughes (1979, 1993) have described the biology of several species.

The American genus *Vermicularia*, with the shell uncoiled, was included in the Vermetidae, but J.E. Morton (1953b) showed it to be a turritellid (Cerithioidea). Similarly, taxa now included in the Siliquariidae (Cerithioidea) were included in the Vermetidae (Morton, J.E. 1951c, 1955a). These differ from vermetids in having a setose operculum, in a lack of septa in the shell, and, in some, in having a median slit and lacking the pedal tentacles.

Vermetids live in intertidal or shallow subtidal habitats, particularly in the tropics, and may be solitary or form dense masses of colonial individuals (for example, Keen 1960b; Safriel 1966). According to R.N. Hughes (1979) this life style presents four problems for vermetids. Firstly, food is limited and there is no ability to move in search of areas of greater food abundance. Secondly, copulation is prevented by the distance between immobile individuals. However, this problem has been overcome by the development of pelagic spermatophores (Hadfield & Hopper 1980). Thirdly, once the juveniles become cemented to the substratum they are unable to move if the environment deteriorates. Finally, there is a danger of smothering by other organisms. R.N. Hughes (1979) considered that in view of these disadvantages there must be a selective advantage in having colonial life. He concluded that at least in some situations, communal nets formed by all individuals in the aggregation would catch more food than single nets. There is also an advantage in reproduction in that the proximity of adjacent individuals increases the chance of reproductive success in a sessile species, and the communal nature of many vermetids allows them to dominate the habitats in which they live.

J.E. Morton (1965) examined evolutionary relationships within the family and summarised several aspects of their biology. Vermetids employ either ciliary mucous feeding, using the gill, or mucous trap feeding as their primary method of obtaining nutriment, or a combination of both (Yonge 1932; Morton, J.E. 1951b, 1951d, 1955a, 1965; Hughes, R.N. 1978, 1985b). In mucous trap feeding, a pedal gland on the foot secretes copious amounts of mucus which is moved along the pair of grooved pedal tentacles to form thin threads. The threads are washed about by the water and become attached to the substratum. As more threads

are produced, a feeding web is formed. The sticky mucus entraps fine particulate matter. With the aid of the radula, the web is ingested and another web is formed. To maximise the time spent feeding, at least some species are able to produce a second web concurrently with the ingestion of the first. Material filtered from the water as it passes over the gills forms a significant second food source (Hughes, R.N. 1985b).

Hadfield & Hopper (1980) reported on the occurrence of spermatophores in seven vermetid species in three genera. Generic and specific differences in the structures were found, but the basic principle is that pelagic spermatophores (Fig. 15.129H) have developed in conjunction with the sessile mode of life. Males release spermatophores into the water column; a few become entangled in the feeding webs of females and are then activated. The activation must occur within a short period (less than 20 hours) if the sperm are to remain viable. As far as is known all vermetids brood their young, with two types of brooding behaviour exhibited by various species. Eggs are brooded in the mantle cavity where they either lie free or are encapsulated, with the capsules attached to the inside of the shell (Hadfield *et al.* 1972; Hughes, R.N. 1978). Larvae are released at the veliger stage or as crawling snails (Morton, J.E. 1951b, 1951d; Barash & Zenziper 1985; Hadfield & Iaea 1989).

Three substantial papers have been published on Australian vermetids. The first was by Yonge (1932), who reported on species on the Great Barrier Reef. Healy (1988a) examined sperm morphology and its systematic implications in the genera *Serpulorbis* and *Dendropoma*. Most recently, R.N. Hughes (1993) reported on the species found at Rottneet Island, Western Australia: *Vermetus* sp.; *Petalconchus caperatus*, *Dendropoma squamifera* and *Serpulorbis siphon*.

Ludbrook (1984) recorded fossils of *Serpulorbis siphon* and *Petalconchus caperatus* in the Quaternary of South Australia. Other fossil vermetids known from the Australian Tertiary are listed by Darragh (1970).

Superfamily CYPRAEOIDEA

Cypraeoideans are popularly known as cowries. There are two families, both represented in the Australian fauna, the Cypraeidae (true cowries) and the Ovulidae (egg and spindle cowries, also known as allied cowries). Feeding habits vary in the group. Cypraeids are herbivores, omnivores, or predators on sponges. Ovulids are specialised host-specific associates of cnidarians. Anatomically this superfamily has much in common with Lamellarioidea and Trivioidea, but lacks the echinospira larval stage that characterises those groups.

The shells of cypraeoideans are usually ovate, glossy-smooth and bilaterally symmetrical, with a narrow almost straight aperture extending the whole length of the ventral side, and terminal anterior and posterior canals. There is no periostracum. The radula is taenioglossate. The pedal ganglion has elongate pedal cords and the osphradium is triradiate. The mantle is bilobed, thin and contractile. Larval development may be direct (in a few cypraeids) or planktotrophic.

Family Cypraeidae

Members of the family Cypraeidae are herbivorous, omnivorous, or sponge-feeders. The shell is usually smooth, spotted and colourful bearing denticles along both the outer and inner lips, never with the spire involute (see Fig. 1.33). Altogether, 77 cowry species are currently recognised in the Australian marine fauna. Of these 14 are endemic. Just over half the Australian species were described by Linnaeus and Gmelin in the 18th Century.

Although the classification of this family has been studied intensively it remains very confused. The classifications that have been proposed have all been based entirely on morphology of the shell, mainly apertural dentition. Over several decades in the mid-20th Century, Franz and Maria Schilder published many

papers on fossil and living cypraeids. In the last of these papers (1971), they recognised four subfamilies, Bernayinae, Cypraeinae, Erroneinae and Erosariinae, each divided into tribes and many genera. The Australian representatives of these genus-level groups are: *Zoila* (Bernayinae); *Mauritia*, *Talparia*, *Cypraea sensu stricto*, *Lyncina*, *Leporycypraea*, *Chelycypraea*, *Luria* (Cypraeinae); *Schilderia*, *Nesiocypraea*, *Umbilia*, *Notocypraea*, *Adusta*, *Erronea*, *Notadusta*, *Palmadusta*, *Blasicrura*, *Bistolida*, *Ovatipsa*, *Cribrarula* (Erroneinae); *Austrocypraea*, *Pustularia*, *Monetaria*, *Erosaria*, *Staphylea*, *Nucleolaria* (Erosariinae). Many of these groups are illustrated by Wilson (1993).

Studies by Kay (1960a, 1960b) on tropical Indo-West Pacific species showed that, although cowries are anatomically quite conservative, the little information available on anatomy and radular morphology cut across the Schilder conchological classification. It appears that there has been extensive convergent evolution in either anatomy or shell morphology, or both. Consequently, Kay and many other subsequent workers elected to return to the Linnaean system, using the generic name *Cypraea* for all species in the Cypraeidae, as an interim measure until there were sufficient anatomical data to resolve the matter. Since then information has become available to enable an attempt at a partial re-classification of the family (Kay 1963, 1985). Several species groups may be recognised, which Kay treats as subgenera of *Cypraea*.

Treatment of all true cowries as *Cypraea* creates some minor nomenclatural problems, but it is convenient for those biologists requiring names for species units. Even though some higher-category relationships among the group are evident, no purpose would be achieved by assigning some species to genera and subfamilies and adopting a partial classification at this time. It is recommended here that Kay's procedure be followed, using other genus-level names (such as those proposed by Schilder) as subgenera of *Cypraea* as an interim measure, and noting higher-category groupings where they are apparent and when it is useful to do so.

The first illustration of a cowry shell appears to have been published by Buonanni in 1681. In 1705, Rumphius illustrated many kinds of cowry from Ambon (Indonesia). These illustrations were cited by Linnaeus (1758) when he introduced the first taxonomically available names for 33 cowry species, under the generic name *Cypraea*. Although none of these species names was based on Australian material, 27 of the species are Indo-West Pacific cowries that occur in northern Australian waters. Later in the 18th Century, Born (1778) named one and Gmelin (1791) named 11 species that occur in Australia. The first cowry to be named from Australian material appears to have been *C. angustata* (Gmelin 1791), an endemic southern Australian species.

During the 19th Century, some 23 species with Australian connections were described, after which discovery of new species slowed in the 20th Century. Only 10 of the new names for Australian cowries introduced during this period are presently considered to be valid, six of them ascribed to Australian conchologists. Between 1960 and 1964 a small magazine called *The Cowry*, devoted entirely to the family, was produced, first in England and later from Port Macquarie, New South Wales, by retired Lieutenant Colonel R.J. Griffiths.

There have been numerous monographs of the family, for example, Gray (1824), Broderip (1837), Swainson (1840), Troschel (1863), Jousseaume (1884), Hidalgo (1906–1907), Schilder (1927), Thiele (1929–1935), Schilder & Schilder (1938–1939, 1971), Burgess (1970, 1985). In Australia, Iredale (1935, 1936b), Steadman & Cotton (1946) and Allan (1956) have published comprehensive reviews, and Wilson & Gillett (1971) and Wilson (1993) have illustrated many species. Until, recently all the taxonomic work was based on shell morphology.

Vayssière (1923, 1927) described the mantle cavities of several cypraeids. Bouvier (1887) and Riese (1931) described the nervous system, and Amaudrut (1898) and Risbec (1937) described the digestive tracts of some species. Schilder (1936) published a

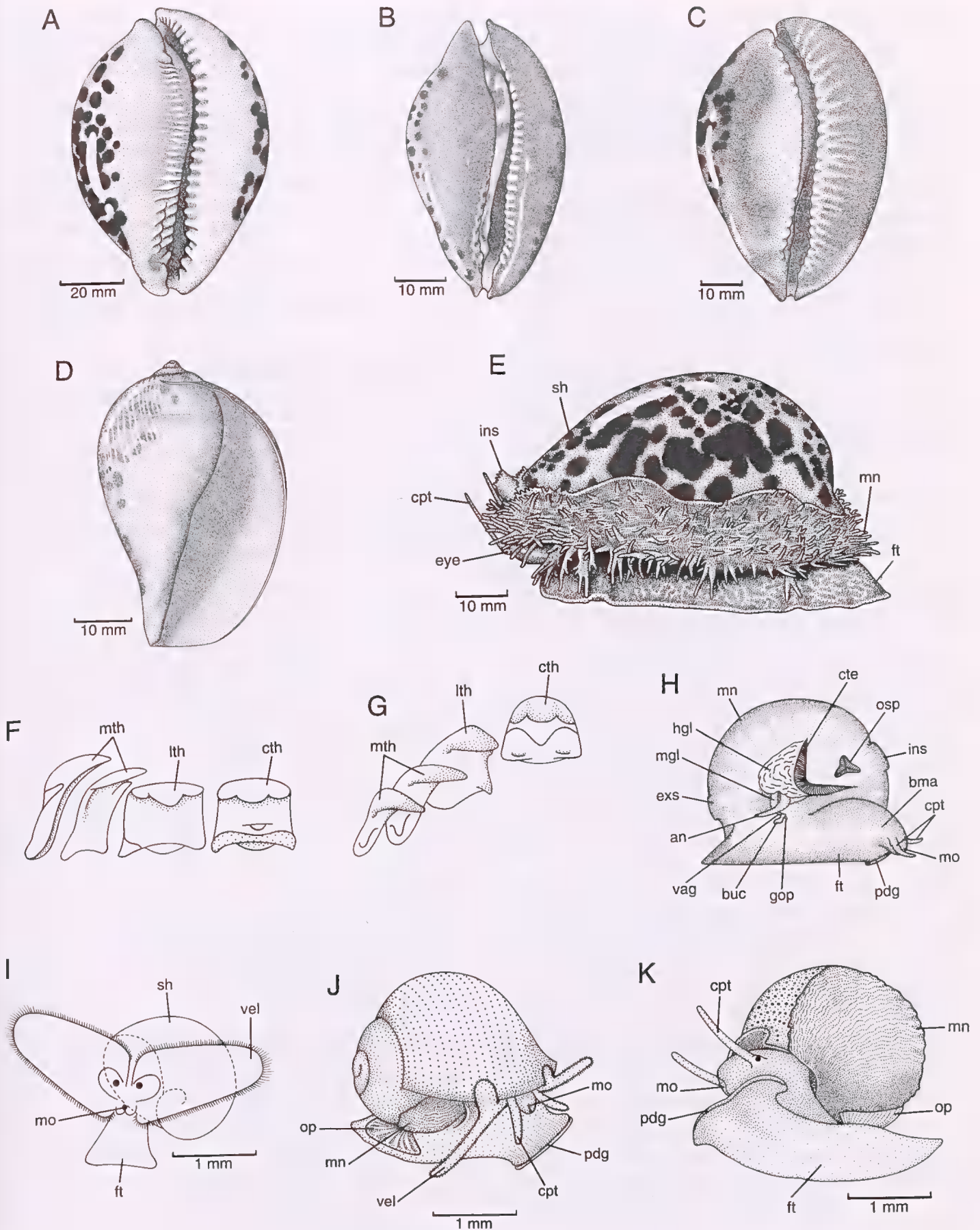


Figure 15.130 Family Cypraeidae. A–C, shells showing apertural dentition, ventral view: A, *Cypraea tigris*; B, *Cypraea (Ziola) friendii*; C, *Cypraea (Ziola) thersites*. D, juvenile shell of *Cypraea (Ziola) thersites*. E, *Cypraea tigris*, lateral view. F, G, half a transverse row of radular teeth: F, *Cypraea caputserpentis*; G, *Cypraea (Ziola) friendii*. H, mantle cavity organs of a female *Cypraea (Ziola) friendii*, drawn from the right side with the shell removed and the right mantle lobe folded up. I, 21 day-old veliger of *Cypraea (Ziola) friendii* extracted from its capsule. J, unhatched 39 day-old embryo of *Cypraea (Ziola) venusta* extracted from its capsule. K, juvenile *Cypraea (Ziola) venusta* 1 day after hatching. an, anus; bma, buccal mass; buc, bursa copulatrix; cpt, cephalic tentacle; cte, ctenidium; cth, central tooth; exs, exhalant siphon; eye, eye; ft, foot; gop, genital aperture; hgl, hypobranchial gland; ins, inhalant siphon; lth, lateral tooth; mgl, mucous gland; mn, mantle; mo, mouth; mth, marginal teeth; osp, osphradium; op, operculum; pdg, anterior pedal groove; sh, shell; vag, vagina; vel, velum. (E, after Wilson & Gillett 1971; F, from Kay 1960a; G, H, after Wilson & McComb 1967; I–K, after Wilson 1985) [C. Eadie]

15. PROSOBRANCHS

condensed survey of the characteristics of the mantle throughout the family. Kay (1960a) described in detail the anatomy of *Cypraea caputserpentis*, and gave information on the anatomy of several other Indo-West Pacific taxa (Kay 1963). Most of these species for which anatomical data are published are tropical Indo-West Pacific cowries, some of which are represented in the northern Australian fauna. The only publication on the anatomy of any of the endemic Australian cowries deals with the subgenus *Zoila* (Wilson & McComb 1967).

Information on the breeding and larval development of several Indo-West Pacific cowries was published by Ostergaard (1950) and Natarajan (1954, 1957). Ranson (1967) described the protoconchs of many species, including some of the Australian endemics, and discussed the implications of his findings on larval development. Wilson (1985) described the egg masses and larval development of several southern Australian endemic cowries.

The shell of juvenile cypraeids is thin, with a wide aperture and a thin outer lip (Fig. 15.130D). At first the spire projects slightly, but as maximum length is attained the last whorl becomes more or less bulbous and, in most species, encloses the spire, the outer lip turns inwards, the whole shell is thickened, and 'teeth' are formed along both margins of the aperture (Fig. 15.130A–C).

Early in development, de-torsion results in the mantle cavity lying along the entire right side of the body. The mantle develops folds at the anterior and posterior ends forming short inhalant and exhalant siphons that correspond to notches in the shell. Water entering the mantle cavity through the anterior siphon passes down the length of the body along the right side of the coiled dorsal visceral mass and exits posteriorly via the posterior canal, it passes the osphradium, hypobranchial gland, ctenidium, excretory and genital apertures, and anus, in that sequence (Fig. 15.130H).

The ventral and lateral sides of the adult shell of many species are especially thickened such that the base becomes broad and a little flattened. Thus, the adult cowry shell is solid, ovate, cylindrical or pear-shaped, tending to be flat-based and round-topped, and with a long, narrow ventral aperture (slightly offset to the right), terminal canals, and transverse ridges or teeth on both the outer and inner lips. Once cowries reach maturity, the shell ceases to increase in size although it may become thicker and heavier. In active animals, the surface of the shell is covered by the contractile, secretory mantle that renders it highly polished (Fig. 15.130E).

The head is broad and bears a pair of lateral tentacles which are usually wide-based, but attenuate terminally. They may be pointed, blunt or clubbed. Prominent eyes are located at the tentacular bases (Pl. 26.6). The foot is wide and flat. When fully extended it may protrude beyond both ends of the shell. Its leading edge is truncate, with a deep transverse groove. The rear end is usually more or less pointed.

The mantle lobes are strongly pigmented and colourful, heavily vascularised, contractile and can slide up and over the dorsal surface of the shell. Where the left and right lobes meet on the dorsum there may be a distinct axial mantle-line in the shell pattern. When the animal is disturbed or inactive the mantle lobes are withdrawn into the aperture. In most cowries (for example, *C. tigris*, Fig. 15.130E), the extended mantle lobes bear projecting papillae or filaments that may be simple or complexly branched (Pl. 26.5). Short siphons are formed by folds in the mantle lobes where they join the midline anteriorly and posteriorly. Their edges may be simple, rolled, serrate, beaded, or fimbriate.

The smallest living species is the Indo-West Pacific *C. minoridens*, which occurs in Queensland waters, reaching a maximum length of about 13 mm. The largest living species is *C. cervus* from Florida and the Bahamas (up to 190 mm). In Australia, the largest cowry is *C. tigris* (up to 150 mm). Some early Tertiary fossil cowries were as large as 350 mm in length. The south-eastern Australian fossil species *C. (Zoila) gigas* grew to as long as 280 mm.

Shells of many cowries are sexually dimorphic, females being, on average, larger than males (Schilder & Schilder 1962). This phenomenon is exhibited by the Australian *C. (Zoila) venusta* (Wilson unpublished data).

Most cowries appear to be herbivorous or omnivorous. Some are specialised browsers on sedentary colonial animals such as sponges and possibly bryozoans. The very common intertidal tropical species *C. caputserpentis* and *C. moneta* are known to feed, at least preferentially, on algae (Kay 1960a; Renaud 1976). Most cowries will graze on algae on the glass of aquaria. It is likely that many, if not most, tropical species are herbivorous.

The species in the Australian subgenus *Zoila* are normally associated with sponges, and some have been observed feeding on them, leaving conspicuous feeding scars. Sponge spicules feature in the stomach contents of the tropical species *C. cribraria* and *C. teres* (Kay 1985). Species of the southern Australian subgenus *Notocypraea* are always associated with sponges on the underside of stones. The south-western Australian species, *C. reevei*, is often found on bryozoans although there is no direct evidence that the tissues are consumed. *Cypraea tigris* and *C. eglantina* have been observed to feed on the flesh of fish or bivalves in aquaria (Kay 1985). The Californian cowry *C. spadicea* was fed on frozen prawn meat in aquaria by Darling (1965). However, whether any cowries are flesh-eating scavengers in nature is not yet known. Information on food and feeding habits of cowries is urgently needed to help clarify the taxonomic relationship of the species.

The alimentary tract of *C. caputserpentis* was described in detail by Kay (1960a). Although minor variations in radular dentition of cowries may be significant for taxonomic purposes, the structure of the radula of *C. caputserpentis* is generally typical of the family (Fig. 15.130F). It is a relatively unspecialised taenioglossate radula serving as a simple raking and scraping tool. The central and lateral teeth are more or less quadrate with a central cusp and smaller lateral cusps. The marginal teeth are elongate, tricuspidate, concave blades (Fig. 15.130F, G). When not in use, the marginals fold inwards over the lateral teeth.

After being transported to the stomach, most of the food ingested by *C. caputserpentis* is held in the posterior cuticular portion; some is carried in a mucous string into the ventral caecum. Digestion appears to be largely extracellular and the presence of strong amylase suggests that the food is largely plant material (Kay 1960a).

The reproductive system has been described in detail for *C. caputserpentis* (Kay 1960a) and species of the Western Australian subgenus *Zoila* (Wilson & McComb 1967). Kay (1963) gave brief descriptions of the genitalia of several Indo-West Pacific cowries.

The female genital tract consists of the ovary, a short renal oviduct, and a long and swollen pallial oviduct. The pallial oviduct is divided by a constriction into a proximal albumen gland and a distal capsule or mucous gland (Kay 1960a). A deep fold forms a strongly ciliated groove running along the antero-lateral edge of the capsule gland, which Kay termed the capsule duct. At the junction between these two glands is a seminal receptacle. In *C. caputserpentis*, the vagina is short and simple, but in *C. (Z.) friendii* there is a thick, muscular sac, the bursa copulatrix, adjacent to the genital aperture.

If present, the bursa copulatrix (as in *Zoila*) appears to be the initial receptacle for sperm. In these species, the 'seminal receptacle' is glandular and appears not to function as a sperm sac. It is inferred that in the absence of a bursa copulatrix (as in *C. caputserpentis*), the penis is inserted some distance into the capsule duct and the seminal receptacle stores the spermatozoa. Thus, the presence or absence of a bursa copulatrix in cowries implies major differences in the way the female genital tract functions; it is likely to be important in classification.

Cypraeids are unusual among gastropods in that the female remains on the egg mass, covering it with her expanded foot until the embryos hatch. The egg mass consists of transparent, oblong or spherical capsules loosely strung or tightly packed together and laid in a depression in the substratum. Each capsule contains many eggs. The majority of tropical cowries have planktotrophic veliger larvae (Fig. 15.130I) that hatch from the capsules after 11 to 18 days (see summary in Wilson 1985). The brooding female remains on the egg mass, presumably without feeding. For the temperate southern Australian species incubation may take six to eight weeks. In aquaria, brooding female *C. (Z.) venusta* accidentally dislodged from their egg mass will climb back and resume their vigil (Wilson 1985). Ostergaard (1950) reported the aggressive behaviour of brooding female cowries of *C. isabella* and *C. helvola*. When disturbed with pencil or forceps the females pressed against the offending object or sharply raised and lowered the shell.

Kay (1960a) has described early development in *C. caputserpentis*. The egg mass is roughly oval, 20–30 mm long and 10–20 mm wide, with three or four layers of capsules embedded in a thick gelatinous matrix. There are between 100 and 200 capsules, each about 1 mm in diameter and containing about 200 eggs. Newly laid eggs are white but they turn yellow as they develop. All of the eggs in the capsules develop. Trochophoral larvae appear within the capsules at about three days and shelled veligers about 15 days after laying. At hatching, the veligers are operculate, with a bilobed velum; they measure about 0.9 mm across the lobes, and swim vigorously. This style of development is characteristic of tropical cowries.

The endemic cowries of southern Australia develop directly (Wilson 1985). *Cypraea (Z.) venusta* of southern Western Australia breeds in October to February. The female lays an egg mass of about 40 mm diameter containing 250 to 300 capsules, stacked two to three deep and embedded in a stiff matrix. The egg masses are laid in depressions in a sponge, or in upturned limpet, abalone or bivalve shells. The capsules are oval and contain several hundred eggs which are orange when freshly laid. Only one egg in each capsule develops. Once the single embryo has reached the veliger stage it begins to consume the remaining uncleaved eggs. The veliger stage is reached in some 15 days or less. At 20 days the embryos have a shell of one whorl, a bilobed velum, and a small foot, but lack head tentacles (cf. Fig. 15.130I). At 39 days (Fig. 15.130J) the velar lobes are small, the left much smaller than the right; the shell is globular, spirally striate and punctate, with two to two and a half whorls, and has an operculum; the mantle lobes spread over the shell; the foot is broad, flat and has an anterior groove; the head is well developed and is equipped with tentacles. Hatching occurs 41 to 48 days after laying (Fig. 15.130K). At hatching the embryos lack velar lobes. They escape from the capsules by bursting the wall with pressure from the anterior end of the larval shell. Once free, the larvae are incapable of swimming but crawl away on the substratum. The mother remains on the egg mass throughout the entire period of incubation.

This type of direct development in which a free-swimming planktotrophic veliger stage is lacking is a feature of all the temperate southern Australian species in each of the endemic subgenera (Wilson 1985). In *C. (Z.) friendii*, incubation time is only about 40 days. In *C. (A.) reevei* and *C. (N.) piperita*, also in southern Western Australia, incubation is about 55 days and 50 days respectively. In *C. (Notocypraea)*, the egg mass contains only 50 to 90 capsules which are oval and loosely connected by thin gelatinous threads. There are no data on development of *C. (Umbilia)*, but the protoconch is paucispiral and thus indicative of direct development (Ranson 1967).

The evolutionary origins of direct development in the four temperate southern Australian cowry subgenera are not understood. It can be no coincidence that it has evolved, apparently independently, in each of these four groups in Australian temperate waters. The temperate South African

subgenus *Cypraeovula*, which may be related to the subgenus *Notocypraea*, also has direct development. The only tropical cowries known to have this kind of development are species thought to be related to the Australian *C. (Zoila)* group.

Wilson & Summers (1966) showed that *C. (Z.) friendii* is characterised by a high degree of inter-population variation in shell morphology, some strongly clinal and some showing no geographic patterns. This may be interpreted in part as a consequence of the lack of a planktonic larval dispersal stage. The species of *Notocypraea* are also characterised by extreme inter-population morphological variation.

There have been no studies on growth rates of Australian cowries. Field observations on *C. (Z.) venusta* in underwater caves of the Marmion Marine Park near Perth, suggest that post-settlement growth may be surprisingly fast, with juveniles reaching full size with in-turned lips in one year (Wilson unpublished data).

Typically, cowries live on firm substrata, on coral reefs or rocks. During the day most species are found clinging to the undersides of coral slabs or stones, or in crevices; at night they roam about in the open. *Cypraea moneta* and *C. annulus* are unusual in that they commonly occur in the open in the intertidal zone even during the day. *Cypraea mauritiana* lives in rock crevices where there is strong wave surge. Some tropical species such as *C. tigris*, *C. carneola* and *C. erosa* seem to prefer shallow clear-water coral reef habitats. A few, such as *C. subviridis* and *C. xanthodon*, live among stones and sponges in turbid waters such as occur on the mainland coast of Queensland.

The majority of tropical cowries may be found in the intertidal and shallow sublittoral zones. However, *C. moneta* and *C. annulus* are almost confined to the intertidal zone, and a few species like *C. hirasei* are found only below 20 or more metres.

The small cowries of the southern Australian subgenera *Notocypraea* and *Austrocypraea* are typical of the family in their under-stone daytime habitat.

The species of the endemic subgenus *Zoila* in Western Australia and South Australia are exceptional in that they live on sponges and do not hide under stones. *Cypraea (Z.) friendii* and *C. (Z.) decipiens* may be found on tall fan-sponges growing on the seabed, or on encrusting sponges growing on rocks. *Cypraea (Zoila) venusta* lives on sponges growing on the walls of underwater caves, but sometimes may be found in the open. *Cypraea (Zoila) marginata* lives in deep crevices of underwater caves where there is little light. All these species live at depths from a few metres to at least 200 m. *Cypraea (Zoila) roselli*, rarely taken in less than 20 m, appears to be a deeper water species, which lives on fan and cup sponges.

Specimens of *Cypraea (Umbilia) hesitata* have been taken in great numbers by trawlers working on sandy substrata along the outer half of the continental shelf, which suggests that they also live in the open, perhaps on sponges or bryozoans. *Cypraea (Umbilia) armeniaca* of South Australia and southern Western Australia has been taken by divers at depths of 30 m or more, living in the open on sponges.

Cowry shells have been used as currency in the African and Asiatic regions since at least the 14th Century B.C., however this practice has ceased in modern times. Nevertheless, commercial trade in cowry shells for ornamental purposes is still commonplace in many Indian Ocean and Pacific countries. In Australia and elsewhere there is a significant commercial trade in specimen cowry shells.

The world distribution of cowries has been documented by Schilder (1965) and Foin (1976). The Cypraeidae are predominantly a shallow-water tropical family. The greatest number of species live in the Indo-West Pacific. Many species, for example, *C. caputserpentis*, are widespread throughout that region from East Africa to French Polynesia, and from southern Japan to the subtropical waters of western and eastern Australia.

15. PROSOBRANCHS

In Australia, cowries conform with the broad biogeographic patterns typical of the marine fauna. The tropical north shares many of the broadly distributed Indo-West Pacific species, whereas in the south there is a suite of species peculiar to the southern Australian region. These two distinct cowry faunas overlap on the east and west coasts. There are only small differences between the tropical cowry faunas of the north-east and north-west.

The fauna of the temperate south of Australia contains four distinct groups of cowries, recognised at the subgeneric level: *Zoila*, *Umbilia*, *Notocypraea* and *Austrocypraea*. *Notocypraea*, with five distinct species, is a feature of rocky shores. *Umbilia* is peculiar to the eastern and southern coasts. *Austrocypraea* species are endemic to the south-western and western coasts. *Zoila* is represented by four extant species in the temperate waters of South Australia and Western Australia and three on the tropical North West Shelf.

The subgenus *Zoila* has Tethyan affinities. It has fossil representatives in the Tertiary of south-eastern Australia, New Zealand, Indonesia and India, and a close relationship with the Tethyan fossil group *Bernaya*. On shell characters, Schilder and Schilder (for example 1971) related both groups to several extinct taxa in the subfamily Bernayinae and to the living *Protocypraea*, *Barycypraea* and *Siphocypraea*, each of which has a Tertiary fossil record and a single relictual extant species. If this is correct, the living species may be regarded as relicts of a flourishing Tethyan group. *Umbilia* has a long lineage in the Tertiary of south-eastern Australia, but apparently no fossil or living members or close relatives elsewhere. It may be regarded as an autochthonous south-eastern Australian group.

Notocypraea has an Upper Tertiary fossil record in south-eastern Australia. The Oligocene-Miocene *Notoluponia* species of the same region and of New Zealand appear to share a common ancestry with *Notocypraea*. There are no fossil or living species elsewhere that appear to be at all closely related. Schilder (1927), however, on the basis of shell characters, related *Umbilia* and *Notocypraea* with the living South African group *Cypraeovula* and the southern Australasian fossil group *Notoluponia*, in the tribe Cypraeovulini. If this is correct, the tribe is likely to have had ancient palaeoaustral origins in the high-latitude Southern Hemisphere (see Fleming 1963).

The position of *Austrocypraea* is enigmatic. The only living species referable to this group is *C. reevei*, which has a late Tertiary to Recent history in southern Australia. Thiele (1929–1935) placed this species in the genus *Lyncina* along with a number of living tropical Indo-West Pacific species. Kay (1963) described the radula of *C. reevei* noting that it resembles those of the species referred to *Lyncina*. However, the anatomy of this species is unknown and its direct development makes this relationship seem unlikely.

The fossil record of tropical Australian cowries is poor. At this stage all that can be said is that the species all have Tethyan origins.

Family Ovulidae

Ovulids are carnivorous cypraeoideans that feed on the polyps of cnidarians (Pls 26.1, 26.2). The shell is pyriform, ovate, cylindrical or lanceolate, sometimes with long anterior and posterior canals; the outer lip may be weakly ridged, but the inner lip is edentulous and smooth, or has a few small posterior denticles. The spire may be involute. The limited information on ovulid anatomy quite clearly demonstrates a close affinity with the Cypraeidae, but the highly specialised habitat and the association with cnidarians distinguishes the Ovulidae.

Rumphius (1705) published the first illustrations of the family when he figured specimens of *Ovula ovum* and *Calpurnus verrucosus* from Ambon. These figures were cited by Linnaeus (1758) when he named these species. The family name, Ovulidae,

was introduced by Fleming (1828). Many authors have used Amphiperatidae, but the generic name *Amphiperas* is unavailable and a junior synonym of *Ovula*, so that Ovulidae becomes the correct family name. The first endemic southern Australian ovulid to be described was *Phenacovolva maccoyi* by Tenison Woods (1878) from Victoria, but no further specimens have been collected since the original material.

Reviews of the family, based entirely on shell characters, have been published by Schilder (1932), Allan (1956) and Cate (1973, 1974). However, the taxonomy of the Ovulidae is far from settled. There are no comparative anatomical data and the shell characters used are trivial and inconsistent. As an arbitrary and provisional guide the arrangement (slightly modified) of Schilder (1932) is given here. The two subfamilies, Ovulinae and Volvinae, are represented in the Australian fauna. Ovulinae are defined as having shells that are pyriform, ovate and inflated, usually with short extremities and the posterior canal turned towards the left. The outer lip teeth are usually well developed and there is a posterior node or ridge called the funiculum on the inflated part of the columella. The anterior terminal ridge is well developed. The genera are *Ovula*, *Primovula*, *Diminovula*, *Margovula*, *Calpurnus* and *Procalpurnus*. The Volvinae are defined as having shells that are fusiform, depressed, with strongly produced extremities. The outer lip teeth are lacking or very weakly developed and the posterior canal turns to the right. Anteriorly there is no terminal ridge. The genera included are *Volva*, *Simnia*, *Phenacovolva*, *Cyphoma* and *Neosimnia*. *Simnia* and *Cyphoma* are found in the Mediterranean, Atlantic and Eastern Pacific. All other genera are found in the Indo-West Pacific Region and are represented in the Australian fauna.

There are more than 100 ovulid species in about 16 genera worldwide; about 46 species have been recorded for the Australian fauna. The Australians, Iredale (1930, 1931, 1936b; three species), Cotton & Godfrey (1932; one species) and Garrard (1963; one species), have described endemic eastern and southern Australian species. In the 1960s and 1970s, the American, Crawford Cate, sometimes with co-authors, named 15 species from Australian localities, especially Queensland.

Juvenile ovulid shells are thin, with a sharp-edged outer lip like the bulla stage of cypraeids. With maturity the outer lip turns inwards and the shell thickens, as in true cowries. However, outer lip teeth are rarely well formed and the columellar lip is always smooth. In the Ovulinae, there is a strong anterior terminal ridge and a posterior thickening (the funicle) on the columellar side which may be nodulose or ridged. In other respects, many ovulid shells resemble those of cowries (for example, Fig. 15.131A–C). In the Volvinae, the anterior and posterior canals may be greatly extended to form long spikes (for example, *Volva volva*, Fig. 15.131D, E) and the funicle and terminal ridge are lacking, or the shells may be spindle-shaped (Fig. 15.131F, G).

Surprisingly, this interesting family has received very little attention. There have been no anatomical descriptions or biological studies of any ovulids from Australia. In recent years, Australian shell-collectors, especially in Queensland, have taken many of the species alive and information is available on the host cnidarians of some species.

Accounts of ovulid anatomy are few. Vayssi re (1923) briefly described anatomy of *Ovula ovum* and *Calpurnus verrucosus*, providing, too, brief notes on the anatomy of Atlantic species of *Simnia* and *Cyphoma*. Ghiselin & Wilson (1965) described the anatomy of the tropical Atlantic genus *Cyphoma*. On this sparse evidence ovulid anatomy appears to resemble that of cypraeids.

In most ovulids, the mantle is brightly coloured and often dramatically patterned. The colours and patterns tend to mimic those of the host cnidarian (Pls 26.1, 26.2). A conspicuous exception is the large *Ovula ovum*, which has a milky-white shell and a thick black mantle. Ovulid mantle papillae are small and simple.

In *Cyphoma gibbosum* there is no evaginable proboscis, only a funnel-like oral area (Ghiselin & Wilson 1965). The jaws are weak. When feeding, the mouth is placed against the surface of the prey and the animal nips at the polyp tissues with the radula and jaws. The gut contains spicules from the cnidarian skeletal structure.

The general features of the internal anatomy, including the gut (Fig. 15.131H), resemble those of cypraeids. *Ovula*, has a large single gland with a duct to the anterior part of the pharynx, but in *Cyphoma* two pairs of glands open under the jaws. These glands may be homologous in the two genera, and may represent salivary glands, although their unusual position suggests that this is improbable. In *Cyphoma* there is, in addition, a pair of oesophageal pouches. Some of the variation in ovulid radular tooth form is illustrated in Figure 15.131I, J. Information on larvae, diet and anatomy of some species is available in the works of Fretter (1951) and Fretter & Graham (1994).

The only details of ovulid reproductive anatomy are those published by Ghiselin & Wilson (1965) for the Atlantic genus *Cyphoma*. The male system is essentially the same as that of cypraeids. The female system differs, however, in having two diverticula opening into the proximal lobe of the pallial oviduct.

One of these is saccular, with a strongly folded and strongly ciliated wall, and was observed to contain many spermatozoa. It appears to be homologous with the seminal receptacle of cypraeids. The other is a stalked, muscular sac that opens into the roof of the proximal lobe. It, too, contains many densely packed spermatozoa. The respective functions of these two sperm-containing organs are unknown. There is no distal bursa copulatrix in *Cyphoma*.

Little is known of the egg laying habits of ovulids. It appears that the females lay a clutch of egg capsules on the surface of the host cnidarians. Gowlett-Holmes & Holmes (1989) reported that the South Australian species, *Primovula heleneae*, lays an egg mass of about 60 colourless, transparent, jelly-like capsules, arranged sequentially and fused together, on a frond of the host gorgonian. Each capsule contains many shelled embryos. The northern Australian species *Calpurnus verrucosus* lays a mass of translucent capsules on its host soft-coral (*Lobophyllum*) and the females appear to brood the eggs beneath the expanded foot in the manner of cowries (Wilson & Gillett 1971, pl. 6). The British *Simnia patula* lays a continuous layer of capsules on its host (*Alcyonium*) covering an area of about 20 mm diameter. Each capsule contains several hundred eggs, all of which appear to develop, the young hatching as veliger larvae (Lebour 1932).

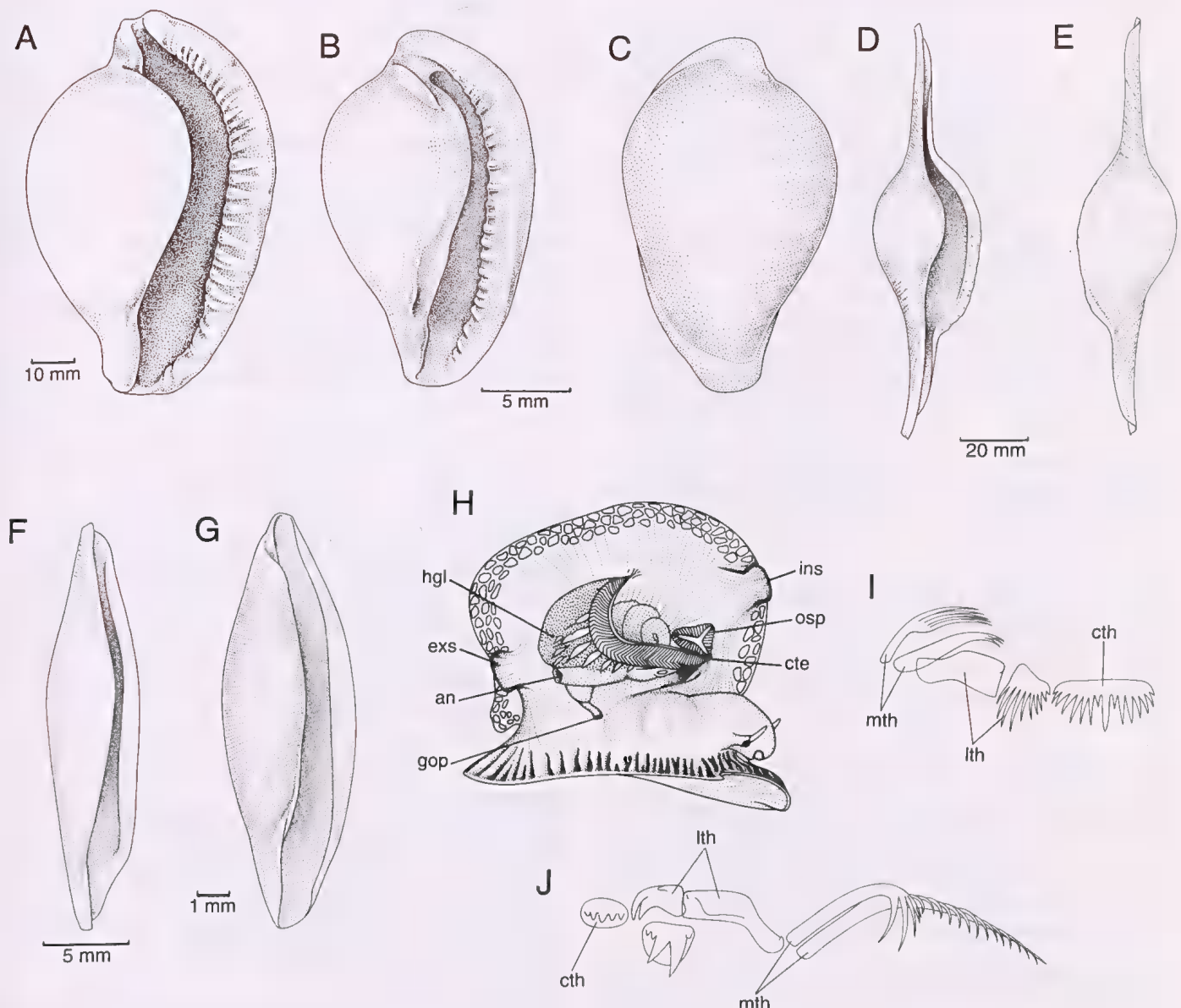


Figure 15.131 Family Ovulidae. Shells: A, *Ovula ovum*, apertural view; B, C, *Primovula pyriformis*, apertural (B) and dorsal (C) views; D, E, *Volva volva* apertural (D) and dorsal (E) views; F, *Volva haynesi*, apertural view; G, *Volva nectarea*, shell, apertural view. H, *Cyphoma gibbosum*, with shell removed, to show the structures in the mantle cavity. I, J, half transverse rows of radular teeth: K, *Pseudocypraea adamsonii*; L, *Jenneria pustulata*. an, anus; cte, ctenidium; cth, central tooth; exs, exhalant siphon; gop, genital opening; hgl, hypobranchial gland; ins, inhalant siphon; lth, lateral tooth; mth, marginal teeth; osp, osphradium. (H, Ghiselin & Wilson 1965; I, J, Thiele 1929–1935) [A–G, R. Plant, H–L, C. Eadie]

15. PROSOBRANCHS

No information is available on the development of Australian ovulids. *Simnia patula* has veligers with four very long narrow velar lobes and a granulose shell with about one and a half simple whorls. There is a characteristic tooth on the outer lip. The long velar lobes may be indicative of a prolonged planktotrophic larval life (Lebour 1932; Fretter & Graham 1962).

There are no detailed Australian studies on any ovulid species. However, observations on the cnidarian hosts have been reported for a few ovulid species, although the host is usually identified only in general descriptive terms. *Ovula ovum* and *Calpurnus verrucosus* live in coral reef habitats and feed on fleshy soft-corals of the genera *Sarcophyllum* and *Lobophyllum*, respectively. *Volva volva* lives on tall slender gorgonians growing on soft substrata. The South Australian *Primovula helenae* lives on the gorgonian *Euplexaura* growing on firm substrata where there are strong currents, and *P. cruenta*, living in the same areas, is an associate of a species of the gorgonid genus *Echinogorgia* (Gowlett-Holmes & Holmes 1989). *Phenacovolva philippinarum* and *Prosimnia semperi* live on species of the gorgonid fan-coral genus *Mopsella* growing on the walls of underwater caves. *Phenacovolva carneopicta* lives on antipatharian 'black-corals' (Rehder & Wilson 1975). Species of *Margovula* are reported to be associated with anemones. These obligatory, apparently host-specific, associations with cnidarians require careful documentation.

Ghiselin & Wilson (1965) described the mating behaviour of *Cyphoma signatum* in an aquarium in Puerto Rico. The male approached the female from the rear, crawled onto the dorsal surface and inserted the penis into the mantle cavity. The pair remained in copula for three and a half hours, during which time there was little movement of either animal. Males and females are frequently found in pairs on one gorgonian.

Ovulids are predominantly tropical; only a few species are temperate. By far the highest species diversity occurs in the central Indo-West Pacific Region, which has many species in common with northern Australia.

Four endemic southern Australian species have been described. *Primovula verconis*, *P. cruenta* and *P. helenae* are recorded so far only from South Australia, but may have wider distributions along the southern coast. There is also an unidentified species of *Phenacovolva* in South Australia.

Ovula ovum is very widespread throughout the Indo-West Pacific Region, extending into the subtropical zone of northern New South Wales on the east coast of Australia and the central west coast of Western Australia. Other smaller and less conspicuous ovulids may have similar wide ranges. However, because of their very specialised and cryptic habits, locality records and distribution data are inadequate in most cases. *Phenacovolva philippinarum* and *Prosimnia semperi* are well-known tropical Indo-West Pacific species that extend far south into the temperate waters of south-western and south-eastern Australia. The former occurs along the whole west coast and as far east as Esperance on the south coast of Western Australia.

Discounting the extravagant taxonomy of some recent authors, it appears that there may be no genera endemic to Australia. The Australian ovulid fauna is typically Indo-West Pacific in its affinities. There are differences at generic level between the tropical Atlantic fauna and that of the Indo-West Pacific. Species of *Simnia* and *Cyphoma* are endemic to the Atlantic, Mediterranean and tropical East Pacific regions, whereas the remaining genera are endemic to the Indo-West Pacific.

The large egg cowry, *Ovula ovum*, has been used traditionally by Pacific Islands people as a decorative item and for ceremonial purposes.

Perhaps because of the specialised habits of ovulids, there are few fossil records. The earliest fossils are species of *Simnia* found in the lower Eocene of Europe. There are several described species of this genus in the Oligocene, Miocene and Pliocene of the

Atlantic and Mediterranean regions. The other Atlantic genus, *Cyphoma*, is represented in the Middle to Upper Miocene and Upper Pliocene of the Caribbean by two fossil species. In the Indo-West Pacific Region, the extant species *Primovula rhodia* is recorded from the Upper Miocene of Japan. The only Australian fossil is *Phenacovolva exigua* from the Upper Miocene of Victoria. Little can be deduced from this sparse fossil record except perhaps that the Ovulidae originated in the early Tertiary and have become speciose in modern warm seas, especially in the central Indo-West Pacific Region.

Superfamily VELUTINOIDEA

This marine superfamily comprises two superficially dissimilar families, the Triviidae (trivias and eratos) and the Velutinidae (velutinids and lamellarias). Triviids have solid, globose, cowry-like shells with a narrow, slitted aperture; velutinid shells, however, are more or less reduced and auriform with a greatly expanded aperture. The grouping of these is based on their possession of double-shelled, echinospira larvae and an array of anatomical features, notably fused mantle lobes (except in *Velutina*), an oval, bipectinate osphradium and a closed vas deferens. In females, a bursa copulatrix is usually absent (present in some Velutinidae). These characters distinguish the superfamily from its nearest relatives, the Cypraeoidea with which, in the past, it has been aligned.

Most recent authors have referred to the superfamily as the Lamellarioidea (or Lamellariacea), but Liltved (1989) pointed out that Velutinidae Gray, 1840 has priority over Lamellariidae d'Orbigny, 1841. No studies have been published on the anatomy or natural history of any Australian species. However, there are detailed accounts of European and South African species (Lebour 1933c, 1933d, 1937; Fretter & Graham 1962; Gosliner & Liltved 1982, 1985, 1987; Liltved 1989) that may be extrapolated to the Australian fauna.

In life, velutinoids resemble cowries in that the mantle spreads over and envelops the shell. The mantle lobes are dorsally bilobed and partially retractile in Triviidae, but completely fused, or nearly so, in Lamellariinae. The mantle is usually brightly coloured and complexly patterned.

Velutinoideans are specialised predators on tunicates. Digestion is aided by enzymes secreted by a pair of fused salivary glands, the ducts of which enter the posterior end of the buccal mass. Hard, chitinous jaws are present in the buccal mass; they are united in Velutinidae, but discrete in Triviidae. The taenioglossate radula usually has a typical 2:1:1:1:2 formula. In some velutinoideans (for example, *Lamellaria* – Behrens 1980; *Coriocella* – Marcus, Ev. 1987), marginal teeth are lacking and the formula is 0:1:1:1:0. The central and lateral teeth are broad and have a pointed triangular central cusp flanked by several denticles. The marginals, when present, are narrow, undivided and may be with or without denticles.

The mobile cephalic tentacles are tactile and have a conspicuous eye near the base. There is a large, elongate, foliose and bipectinate osphradium. This is an important character distinguishing the group from the Cypraeoidea in which the similarly large osphradium is triangular and tri-radiate. The central nervous system is highly concentrated with largely untwisted lateral cords (Gosliner & Liltved 1985) and the pedal ganglia are rounded. At one time the rounded pedal ganglia were thought to be elongate (Shaw 1909), but this has been shown to be incorrect (Gosliner & Liltved 1985).

Some velutinoidean reproductive systems have been described by Lebour (1933c), Fretter & Graham (1962), Gosliner & Liltved (1982, 1987), Ev. Marcus (1987) and Liltved (1989). Some species are protandrous or simultaneous hermaphrodites and others have separate sexes. In protandrous species the male system develops first.

Males of gonochoristic species have a genital system that generally resembles those of cypraeoideans, comprising a testis, ampulla, vas deferens and penis. There is usually a glandular swelling, the prostate gland, at the position where the vas deferens emerges from the visceral mass into the mantle cavity. Unlike the cypraeoidean arrangement, however, the outer part of the vas deferens is a tubular (closed) ciliated duct running across the right side of the foot to the broad, tapering, muscular penis.

Females of gonochoristic species have a glandular oviduct leading from the ovary to the genital aperture on the right side of the mantle cavity. It comprises three major lobes: the albumen, capsule and mucous glands. Only rarely is there a bursa copulatrix, sperm being deposited during mating directly into the oviduct and stored in a seminal receptacle. The receptacle has an unusual position, arising from the albumen gland or between it and the capsule gland.

Flask-shaped egg capsules are laid in holes bitten into the test of compound ascidians upon which the snails prey (Lebour 1933c, 1933d; Fretter & Graham 1962). *Trivia* species have a ventral pedal gland that moulds the capsules and a ventral papilla that assists emplacement of capsules in the hole. A ventral pedal gland is also present in the velutinid *Coriocella* (Liltved 1989), but not in *Lamellaria* (Fretter & Graham 1962). The capsules of the British species *T. monacha* are about 5 mm high (Fig. 15.24), those of *Lamellaria perspicua* a little smaller. The capsules open through a narrow, funnel-like neck that projects a short distance above the surface of the ascidian; a plug seals the capsule opening until hatching.

Gosliner & Liltved (1982, 1987) noted that southern African *Trivia* shells have large protoconchs, indicating that development in these temperate species may be direct. Detailed information on development is available for Atlantic species of *Velutina*, *Lamellaria*, *Trivia* and *Erato* (for example, Lebour 1931, 1933c, 1933d, 1935; Fretter & Graham 1962) which produce planktotrophic echinospira larvae (see Fig. 15.30). The larval shell has two layers of conchiolin separated by a fluid-filled space. The outer layer, is thin, colourless, glassy and transparent and the inner layer is reinforced with calcareous matter. In *Trivia* and *Erato*, the two shell layers are coiled helically, but in the Velutinidae the outer shell is planispiral and the inner one helicoid. The outer, periostracal layer is shed at the time of metamorphosis.

The inner layer of the echinospira shell was once thought to represent the true shell and the outer layer to be an accessory shell, known as the scaphoconch. The current view (Fretter & Graham 1962) is that the two 'shells' are merely the periostracal and calcareous parts of the normal gastropod shell, separated to a greater degree than usual. In all gastropod veliger larvae, the two layers are secreted by rings of gland cells at the mantle edge and formation of the outer conchiolin layer, which later becomes the periostracum, precedes formation of the inner calcified layer. During echinospira larval development the growing edges of the shell-secreting glands diverge, exaggerating the separation of the two layers so that their union to form a single shell cannot occur.

The four velutoidean subfamilies, that is, Velutiniinae and Lamellariinae comprising the Velutinidae, and the Triviinae and Eratoinae, comprising the Triviidae, have been aligned with each other and with the Cypraeoidea in various combinations, but they are currently regarded as components of a distinct superfamily characterised most notably by having an echinospira larva (Fretter & Graham 1962; Gosliner & Liltved 1985; Ponder & Warén 1988; Liltved 1989; Wilson 1993). With one known exception, echinospira larvae are confined to the Velutinoidea. The exception is the British capulid, *Capulus ungaricus* (Lebour 1937). It is unclear whether this larval form is typical of the Capulidae or whether it has evolved independently in the group. If the former, it could represent evidence of phylogenetic relationship between capuloideans and the Velutinoidea.

Family Triviidae

Shells of the family Triviidae are either globose, prominently ribbed and with a narrow, toothed aperture in Triviinae (bean cowries) or tumidly conical and smooth with a narrow, toothless aperture in Eratoinae (eratos). The colourful mantles are fused anteriorly and posteriorly, but have divided, retractile lobes that may meet dorsally to envelop the shell (Pl. 26.4), as in cypraeoideans. There is no periostracum or operculum in adults.

Most described Australian triviids were named in the 19th Century by European or American workers, often from non-Australian material. There have been no systematic reviews of Australian trivias or eratos other than the general accounts of Allan (1956) and Wilson (1993) and the world monographs of Schilder (1933 – Eratoinae) and Cate (1979 – Triviinae). The nomenclature and biogeography of the Australian species are confused and additional species certainly remain to be described.

The globose form of triviine shells, and their involute spire and elongate, slit-like aperture with notched anterior and posterior canals (Fig. 15.132C, D) led to their vernacular name of bean cowry, and to their grouping with the Cypraeidae in most older classifications. A typical, but not universal feature is the extension of the apertural 'teeth' ridges over the sides and dorsum of the shell. There may or may not be an axial sulcus (groove) on the dorsum. Typically the shells are white, but there may be small blotches of colour on the dorsum.

Erato shells tend to be tumidly conical with an exsert spire (Fig. 15.132A, B). They are smooth except for small teeth along the edge of the outer lip and inner (columellar) lip. Eratos are also generally white or cream, but often have pale pink, purple or brown extremities and may be faintly spotted or blotched.

The mantle is bilobed, and in some species of *Trivia* the rigidity of the mantle lobes is increased hydrostatically (Liltved 1989). Some species, at least, secrete acid from the mantle (Thompson 1961). Both siphons are fused to the mantle. The inhalant siphon is long and, in active animals, is held aloft at an incline, but the posterior siphon is merely a short rim bordering the posterior canal of the shell. Cephalic tentacles are long and cylindrical or attenuate; in *Trivia* the tentacles are grooved dorsally (Liltved 1989). The foot is large and flat with a wide, arcuate, thickened anterior end and a long attenuate, trailing posterior end; the anterior end is transversely grooved and glandular. Trivias and eratos are fast moving snails. Aspects of internal anatomy are illustrated in Figure 15.132E, and features of the radula teeth in Figure 15.132I.

Generally the reproductive system (Fig. 15.132F, G) is as described for the superfamily, but structural variability is present within the Triviidae, particularly in the position and elaboration of the seminal receptacle in males (Gosliner & Liltved 1982, 1987). Most species have separate sexes, but some are, unusually for caenogastropods, hermaphrodites (Gosliner & Liltved 1982, 1987). Egg capsules are deposited with the host.

The flask-shaped egg capsules of *Trivia monacha* were described in detail and figured by Fretter & Graham (1962, p. 408, fig. 214). The echinospira larvae of the British *Trivia monacha* (Fig. 15.132H) and *Erato voluta* were described and figured by Fretter & Graham (1962) after (Lebour 1931). In both these species, the inner and outer shell layers are helicoid and smooth, and there is a bilobed velum. In *T. arctica* the velum is 4-lobed. There is a large operculum which is lost during metamorphosis.

The Triviinae are a cosmopolitan subfamily with many species in the tropics and a few in temperate seas. There is a concentration of temperate species in southern Africa (Liltved 1989). Wilson (1993) listed 11 Australian species, most of them widespread in the tropical Indo-West Pacific Region. There is one described southern temperate species, *Trivia merces* (Pl. 26.4), which also occurs in New Zealand.

15. PROSOBRANCHS

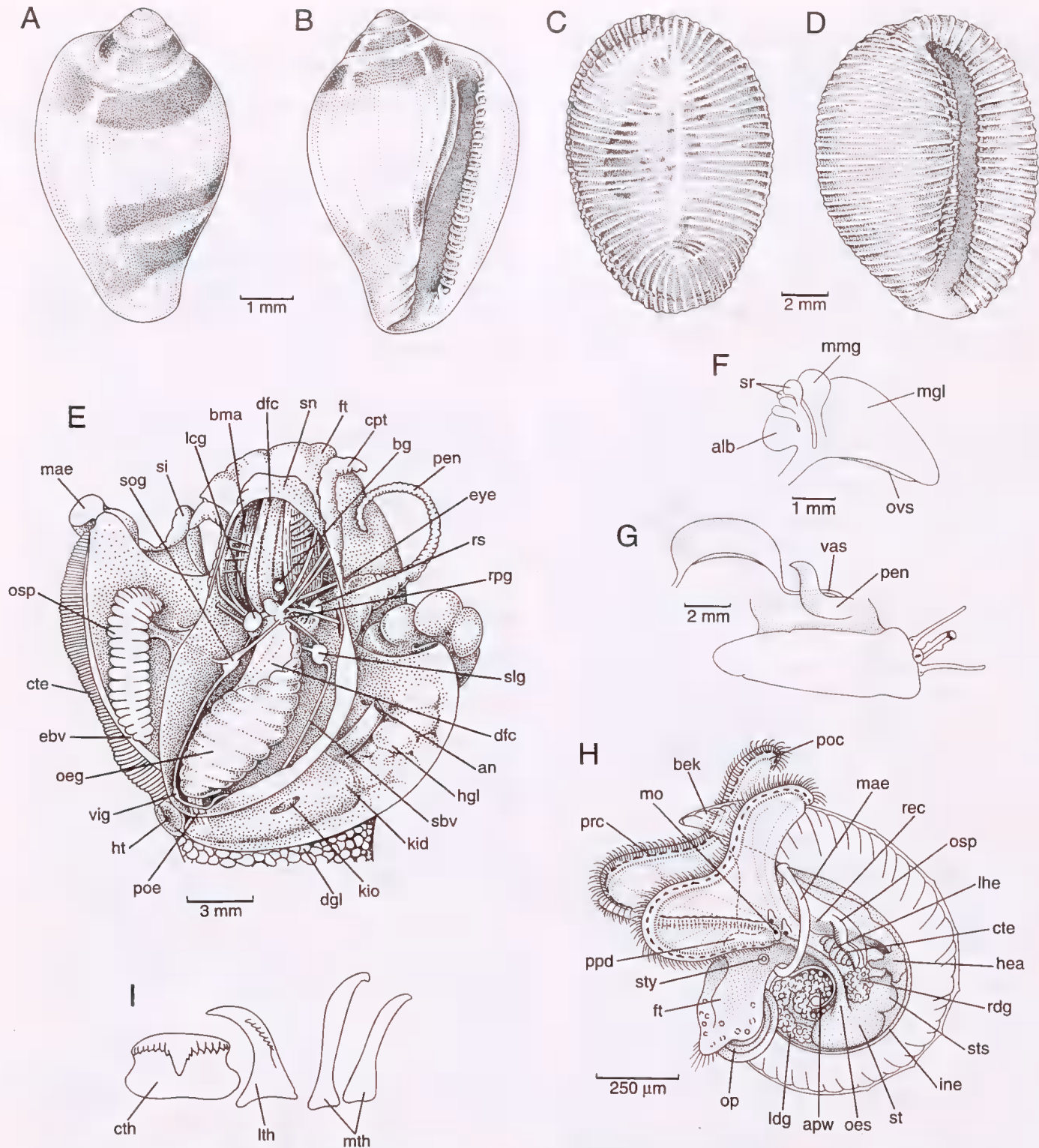


Figure 15.132 Family Triviidae. **A, B**, shell of *Proterato lachryma*: **A**, dorsal view; **B**, apertural view. **C, D**, shell of *Ellatrivia merces*: **C**, dorsal view; **D**, apertural view. **E**, *Trivia monacha*, dissection of mantle cavity and anterior part of body. **F, G**, *Trivia pellucidula*, reproductive systems: **F**, female; **G**, male. **H**, *Trivia monacha*, echinospira larva. **I**, *Trivia calvaricola*, half a transverse row of radular teeth. **alb**, albumen gland; **an**, anus; **apw**, apical whorl; **bek**, beak; **bg**, buccal ganglion; **bma**, buccal mass; **cpt**, cephalic tentacle; **cte**, ctenidium; **cth**, central tooth; **dfe**, dorsal food channel; **dgl**, digestive gland; **ebv**, efferent branchial vessel; **eye**, eye; **ft**, foot; **hea**, definitive heart; **hgl**, hypobranchial gland; **ht**, heart; **ine**, inner part of echinospira shell; **kid**, kidney; **klo**, kidney opening; **lbg**, left cerebral ganglion; **ldg**, left lobe of digestive gland; **lhe**, larval heart; **lth**, lateral tooth; **mae**, mantle edge; **mgl**, mucous gland; **mmg**, membrane gland; **mo**, mouth; **mth**, marginal teeth; **oeg**, oesophageal gland; **oes**, oesophagus; **op**, operculum; **osp**, osphradium; **ovs**, oviducal slit; **pen**, penis; **poc**, postoral cilium of velum; **poe**, posterior oesophagus; **ppd**, propodium; **prc**, preoral cilium of velum; **rdg**, right lobe of digestive gland; **rec**, rectum; **rpg**, right pleural ganglion; **rs**, radular sac; **sbv**, suboesophageal part of visceral loop; **sl**, siphon; **slg**, suboesophageal ganglion; **sn**, snout; **sog**, supra-oesophageal ganglion; **sr**, seminal receptacle; **st**, stomach; **sts**, style sac; **sty**, statocyst; **vas**, vas deferens; **vig**, visceral ganglion. (**E, H**, after Fretter & Graham 1962; **F, G, I**, after Gosliner & Liltved 1987) [**A–E**, R. Plant; **F, G, I**, I. Hallam; **H**, C. Eadie]

The Eratoinae are a smaller group. Schilder & Schilder (1971) listed 23 species worldwide, six of which were listed from Australia by Wilson (1993). The Australian species are in the genera *Proterato* and *Hespererato*, and are described from the east and south coasts of Australia. The apparent absence of the subfamily on the Indian Ocean side of the continent is probably the result of inadequate sampling. Both subfamilies are represented in the Middle and Upper Tertiary deposits of south-eastern Australia.

The similarity of triviid and cypraeid shell form has often led to the Triviidae being classified as a family of the Cypraeoidea. Eratos, on the other hand, with their conical shells are more like marginellids and have usually been treated separately. However, the larval type and anatomical details of trivias and eratos are virtually indistinguishable and they are now regarded as members of the same family, allied to the Velutinidae rather than to cypraeoideans.

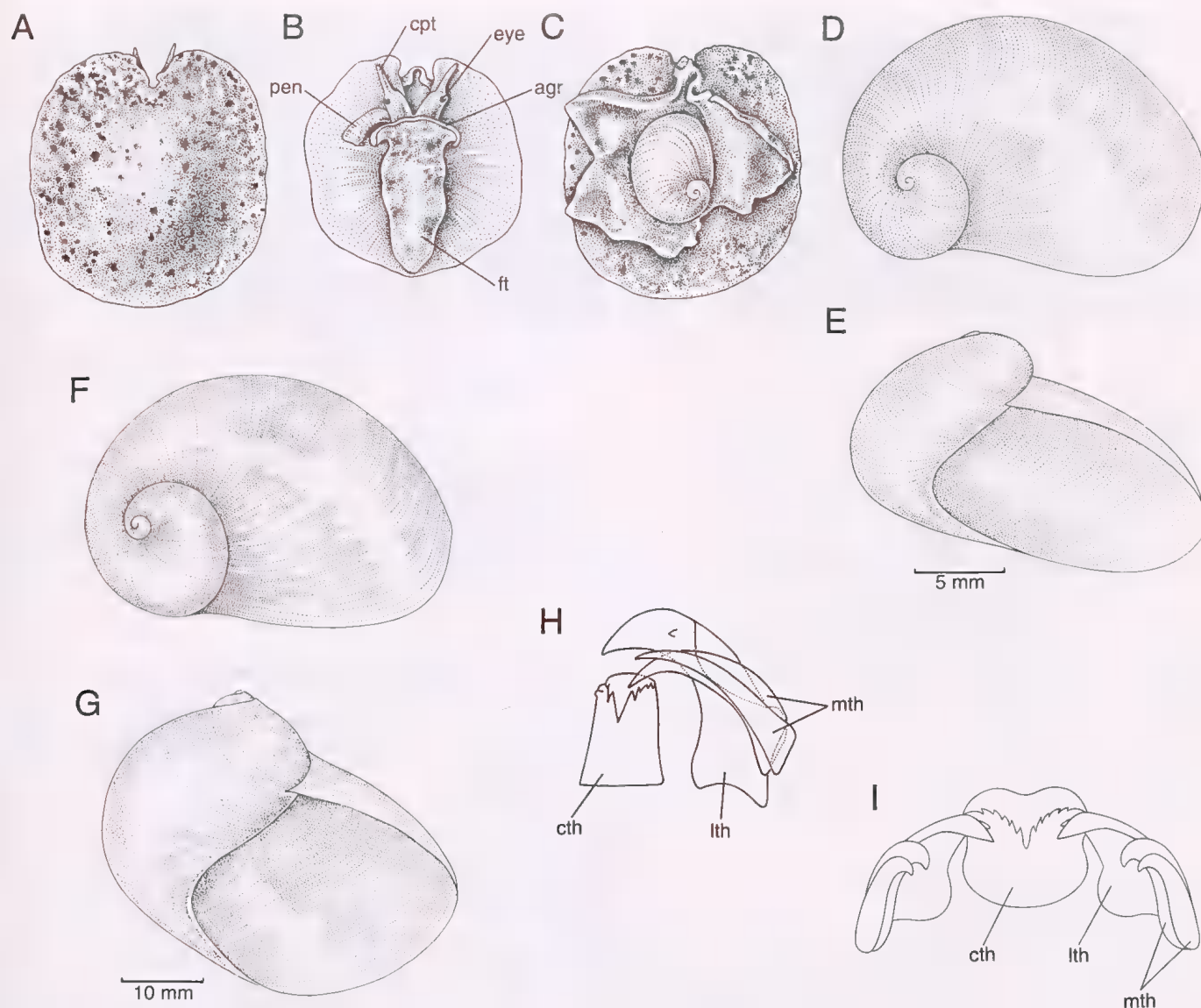


Figure 15.133 Family Velutinidae. A–C, *Lamellaria* sp., external appearance and view of internal shell: A, animal, dorsal view; B, animal, ventral view; C, mantle cut to expose internal shell. D, E, *Lamellaria ophione*, shell: D, dorsal view; E, apertural view. F, G, *Mysticoncha wilsoni*, shell: F, dorsal view; G, apertural view. H, I, portions of radulae: H, *Marseniopsis pacifera*, half of a transverse row of radular teeth; I, *Mysticoncha wilsoni*, a single transverse row of radular teeth. agr, anterior groove; cpt, cephalic tentacles; cth, central tooth; eye, eye; ft, foot; lth, lateral tooth; mth, marginal teeth; pen, penis. (A–C, after Allan 1958; H, after Thiele 1929–1935; I, after Basedow 1905)

Family Velutinidae

Velutinid shells are thin, depressed and have a wide, expanded aperture (Fig. 15.133D–G). Australian Velutinidae have seldom been studied. Smith (1886) named an eastern Australian species (collected by the Challenger Expedition) that was subsequently designated as the type species of *Mysticoncha* by Allan (1936). Basedow (1905) described a number of southern species of *Lamellaria* (most of which he erroneously attributed to *Caledoniella* which is a genus belonging to the Hipponicoidea). Allan (1936, 1958) carried out some investigations of the shells, radulae and animals of east coast species and Iredale (1936b) named some New South Wales species of *Marseniopsis* based only on shells. There has been no recent review of these Australian taxa and some may prove to be widely distributed species named from other areas. Nor has there been any anatomical or biological study of Australian velutinids although detailed information is available on Atlantic species of *Velutina*, *Lamellaria* and *Marsenina*, and on the Indo-West Pacific genus *Coriocella* which is known from northern Australia.

The shell of *Velutina* species is moderately thin and not enclosed by the mantle; it has a velvety periostracum. The animal can withdraw into the shell. In the Lamellariinae, the shells are thin, flattened and auriform and are entirely or almost entirely

enveloped by the large fleshy mantle. Lamellariines are slug-like in appearance with a wide foot that is arcuate anteriorly and stoutly attenuate posteriorly (Fig. 15.133A–C). Unlike that of the Triviidae, the lamellariine anterior siphon is short. In most genera the mantle is fused dorsally and is not retractile, although a small pore has been reported in some *Lamellaria* species (Ghiselin 1964; Behrens 1980). Species of *Marsenina* are an exception, in that there is a dorsal pore or fissure and the mantle lobes are partially retractile. Radular tooth form is illustrated in Figure 15.133H, I.

Velutina species are simultaneous hermaphrodites. Sperm and ova are produced in different acini of the gonad and the genital duct is complexly divided (Fretter & Graham 1962, p. 373, fig. 194C). Within the Lamellariinae both hermaphroditic and gonochoristic reproduction occurs. The genus *Marsenina* is hermaphroditic (Bergh 1853, 1886a, 1886b). Sexes are separate in *Lamellaria* (Fretter & Graham 1962), *Coriocella* (Marcus, Ev. 1987; Liltved 1989) and *Marseniopsis* (Behrens 1980). The penis of the British species *Lamellaria perspicua* has an unusual modification for inserting sperm into the upper parts of the female pallial oviduct – it has a stout, laterally compressed basal region and a slender apical part that arises from the base subterminally and is set at right angles to it (Fretter & Graham 1962, p. 156, fig. 94).

15. PROSOBRANCHS

As in the Triviidae, ova are laid in flask-shaped capsules within the test of the ascidian prey. The capsule of *Velutina* has been described and figured by Diehl (1956), and that of *Lamellaria perspicua* was described in detail and figured by Fretter & Graham (1962). Each capsule contains 1000–3000 ova. Unlike *Trivia*, in *Lamellaria* there is no ventral pedal gland for moulding the capsule as it emerges from the oviduct.

Echinospira larvae of Velutinidae have been described by Lebour (1931, 1935), Giard (1875), Simroth (1895, 1911), Pelseneer (1911), Fretter & Graham (1962) and McCloskey (1973). The two shells of the echinospira larva lie in different planes. The outer shell is planispiral, the inner one helicoid. In *Velutina* the outer shell is smooth and rounded, but in Lamellariinae it is sharply carinate around the periphery. The larval velum is bilobed in *Velutina*, but six-lobed in the known species of *Lamellaria*.

The mantle and foot of Lamellariinae are brightly coloured and patterned (Pl. 26.3). These animals are notable examples of concealment by mimicry of the prey upon which they live (Ghiselin 1964). The flattened shape of *Lamellaria* gives the animals the appearance of a bulge on the surface of the ascidian colony and the colour and pattern of the snail often so closely mimic the surface of the prey that they are easily overlooked.

The Velutininae are not recorded from Australian waters, but the Lamellariinae are well represented by the genera *Lamellaria*, *Marseniopsis*, *Mysticoncha* and *Coriocella*. *Lamellaria* and *Marseniopsis* are cosmopolitan genera, the former with at least five species in southern Australian waters where they are a conspicuous, though unstudied element in the intertidal fauna of rocky shores. *Mysticoncha*, a genus of uncertain taxonomic status, occurs in south-eastern Australia and New Zealand. *Coriocella* is a widespread Indo-West Pacific genus with at least one species on the tropical shores of northern Australia.

Superfamily NATICOIDEA

The Naticoidea is a group of carnivorous, burrowing marine caenogastropods comprising one family, the Naticidae (Triassic–Recent). Naticoids are best known for their shell-boring predation using an accessory boring organ on the proboscis (Fig. 15.135B), and for the production of egg collars impregnated with sand or a gelatinous substance. The first of these features, however, was apparently absent in Jurassic and early Cretaceous genera. Extant species are adapted for burrowing. They have very short cephalic tentacles, an extension of the propodium which functions as a head shield, and a metapodial flap. These structures at least partly cover the shell. The alimentary canal is modified for carnivory, having a proboscis, a large oesophageal gland and a simplified stomach. The operculum usually fills the aperture and may be horny or calcareous.

Family Naticidae

Species of the marine family, Naticidae, commonly known as moon shells, have globose to pyriform shells that are usually smooth and often have colour patterns (Pl. 27.1). No monographs deal specifically with Australian naticids, but the revisions of Cernohorsky (1971), Kilburn (1976), Majima (1989) and Kabat (1990b) include several tropical Australian species. Little information is available on the temperate and cold water naticids of southern Australia; some are known only from the original descriptions although important observations on the taxonomy of temperate naticids from Australasia (particularly New Zealand) were made by Finlay & Marwick (1937).

The shells of naticids are dextral and moderate to low-spired (Fig. 15.134D–F, I), except for *Sinum* which is nearly auriform (Fig. 15.134G, H); the maximum dimension is rarely over 70 mm. Most taxa are umbilicate, and the last whorl and aperture are greatly enlarged. The outer lip of the aperture is not sculptured, and the inner lip is usually thickened with umbilical and parietal calluses that may partially or completely fill the umbilicus. A funicle (rib) is present within the umbilicus in the Naticinae.

Four subfamilies have been recognised in 'traditional' (non-cladistic) classifications of the Naticidae: Ampullospirinae, Polinicinae, Sininae and Naticinae. Ampullospirinae and Polinicinae are paraphyletic grades. The Ampullospirinae have channelled or tabulate whorls and are geologically the oldest subfamily; the Polinicinae have smooth shells with a corneous operculum (Fig. 15.134B, J); the Sininae typically have spirally striate shells (Fig. 15.134A, G, H) with a corneous, reduced to vestigial, operculum; the Naticinae have smooth or ribbed shells with a calcareous operculum (Fig. 15.134C, K).

All naticids are predatory. The molluscan prey are captured with the dilated foot, and the radula is used in combination with the acid-secretory proboscoideal accessory boring organ (often referred to as ABO in the literature) to bore or drill a countersunk hole in the prey shell through which the prey flesh is consumed (Kabat 1990a for review). The taenioglossate radula is of the basic pattern, the central tooth having one central and several lateral cusps and a basal ridge (Fig. 15.135C). The lateral teeth are usually multicuspidate, and the marginal teeth are narrow and pointed. Salivary and oesophageal glands are present. The bipectinate osphradium has enlarged and folded leaflets. The cephalic tentacles are short and the eyes are very small or lost. Other morphological features largely conform with the basic neotaenioglossan body plan (see also Fretter & Graham 1962, 1994).

Naticids feed by wrapping their prey (usually a mollusc) in their foot. Shells of prey are often bored in characteristic positions determined by the way the particular species of prey is most effectively held (Bayliss 1986), or in the thinner parts of the shell (Ansell & Morton, B. 1987; see also Kabat 1990a; Fretter & Graham 1994).

Reproduction in Australian naticids is documented only for members of the exceptional genus *Conuber*. Naticids are dioecious and fertilisation is internal. Some taxa have a grooved (open) penis (Fig. 15.135A). The embryos are laid in a diagnostic sand collar (egg case), an agglutinated circular mass of sand, mucus, and egg capsules (Fig. 15.135D) which remains on the sandy sublittoral surface until hatching occurs. Planktotrophic, lecithotrophic, and direct developmental modes all occur in this family. *Conuber* produces gelatinous sausage-shaped egg masses lacking sand, but otherwise similar to those of the other naticid taxa (Murray 1963, 1966; Smith, Black & Shepard 1989). Longevity has been reported for only one Australian species, *Conuber sordidus*, which lives for five years (Rainer 1982).

The large foot, with its propodial and metapodial flaps, is characteristic of the family. In some taxa, this totally envelops the shell (for example, *Sinum* species, Fig. 15.134A). The mantle cavity is protected, as the animal burrows, by a propodial flap; and posteriorly, a flap from the metapodium also extends over the shell (Fig. 15.134C). The foot has a water vascular system (Russell-Hunter & Apley 1968; Russell-Hunter & Russell-Hunter 1968) which aids in expansion; water is ejected from pores around the edge on contraction (Zeigelmeier 1958). The details of this 'water-vascular' system, however, are still obscure. Russell-Hunter & Russell-Hunter (1968) showed that the weight of a fully expanded naticid was 3.5 times that of a contracted one, most of this weight change being due to the uptake of water into the foot.

Naticids are common in the sandy and muddy areas of the intertidal and sublittoral zones, actively burrowing (see Trueman 1968 for details of burrowing process) through the substratum in search of molluscan prey. Some taxa are primarily nocturnal; others are known to hunt at the substratum surface in intertidal zones at low tide. Their chief predators are bottom-dwelling fish (especially small sharks and skates), crabs and other naticids.

Naticid behaviour has been studied primarily in conjunction with analyses of predation (see Fretter & Graham 1994 for summary) and reproduction. Kitching modelled the tracks of the Australian *Conuber incei* and suggested that prey detection occurs in part by mechanoreception (in addition to chemosensory modes) (Kitching

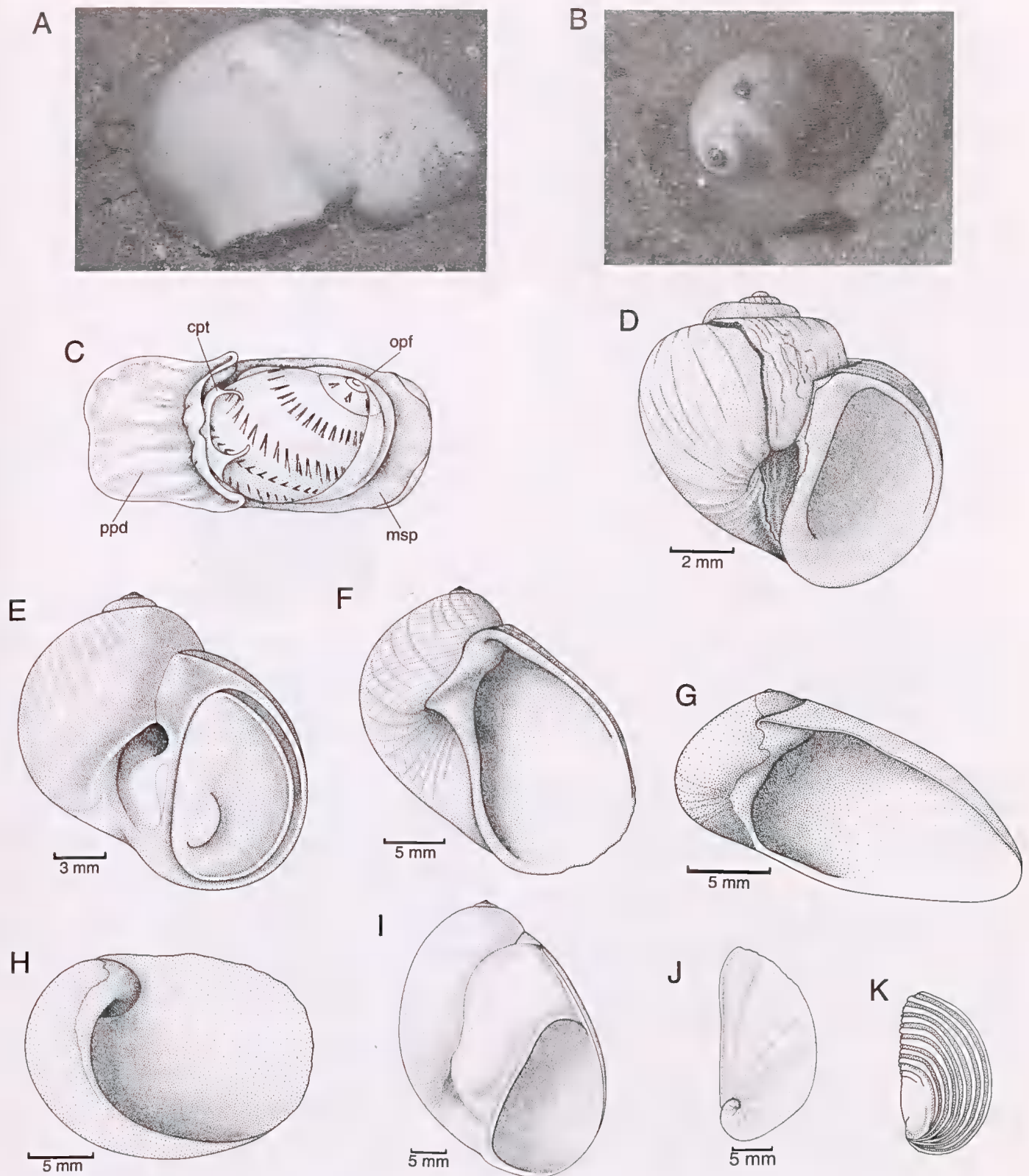


Figure 15.134 Family Naticidae. A, *Sinum zonale*, external appearance. B, *Conuber sordidus*, external appearance. C, *Euspira catena*, animal creeping, parts of the foot shown. D–I, shells, apertural (D–G, I) and ventral (H) views: D, *Friginatica beddomei*; E, *Notocochlis gualtieriana*; F, *Eunaticina papilla*; G, H, *Sinum zonale*; I, *Polinices mammilla*. J, K, opercula: J, *Polinices mammilla*; K, *Naticarius onca*. cpt, cephalic tentacle; msp, mesopodium; opf, opercular fold of metapodium; ppd, propodium. (C, after Fretter & Graham 1962; K, after Cernohorsky 1971)

[A, K.L. Gowlett-Holmes; B, L. Newman & A. Flowers; C, R. Plant; D–J, C. Eadie; K, I. Hallam]

& Pearson 1981; Kitching & Zalucki 1982). As predators, naticids may have a destructive influence on commercial shellfish beds and other economic sources of edible bivalves.

The family is distributed worldwide, with the greatest species diversity in tropical regions. Approximately 40 extant genera and over 250 species are known worldwide, with many of the taxa little studied. At least 15 genera and about 70–75 species in the

four subfamilies occur in Australian waters. These include the endemic *Conuber* (four species), *Friginatica* (three species), and *Tasmatica* (one species); the warm temperate to tropical *Eunaticina* (six species), *Glossaulax* (one species), *Mammilla* (six species), *Natica* (six species), *Naticarius* (six species), *Notocochlis* (five species), *Polinices* (nine species), *Sigatica* (two species), *Sinum* (five or six species), *Tanea* (eight species), *Tectonatica* (five species); the temperate to cold water *Euspira*

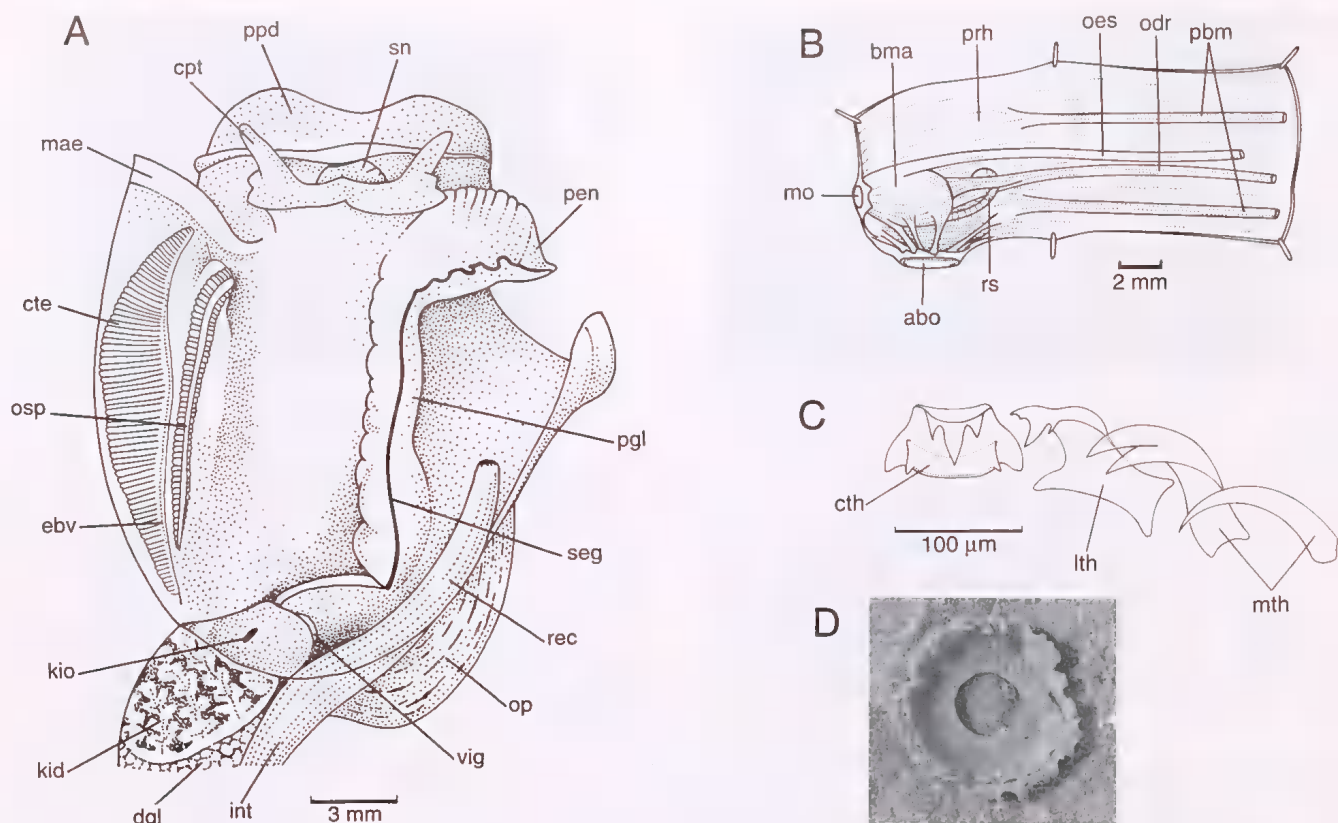


Figure 15.135 Family Naticidae. **A**, *Euspira catena*, male with the mantle cavity opened dorsally. **B**, proboscis of *Neverita duplicatus*, opened laterally to show the relationship of the accessory boring organ to the buccal mass. **C**, half a transverse row of radular teeth of *Euspira catena*. **D**, *Polinices* sp., egg case. **abo**, accessory boring organ; **bma**, buccal mass; **cpt**, cephalic tentacle; **cte**, ctenidium; **cth**, central tooth; **dgl**, digestive gland; **ebv**, efferent branchial vessel; **int**, intestine; **kid**, kidney; **kio**, kidney opening; **lth**, lateral tooth; **mae**, mantle edge; **mo**, mouth; **mth**, marginal teeth; **odr**, odontophoral retractor muscle; **oes**, oesophagus; **op**, operculum; **osp**, osphradium; **pbm**, proboscoidal retractor muscle; **pen**, penis; **pgl**, prostate gland; **ppd**, propodium; **prh**, proboscoidal haemocoel; **rec**, rectum; **rem**, retractor muscle; **rs**, radular sac; **seg**, seminal groove; **sn**, snout; **vig**, visceral ganglion. (**A**, after Fretter & Graham 1962; **B**, after Carriker 1981; **C**, after Cernohorsky 1971) [A, R. Plant; B, C. Eadie; C, I. Hallam; D, L. Newman & A. Flowers]

(one species); and several species of uncertain generic placement. The naticid species of Queensland, Northern Territory and the northern part of Western Australia often also occur elsewhere in the tropical Indo-Pacific; by contrast, those of southern Australia are usually endemic.

Naticids have an excellent fossil record overall (Triassic to Quaternary), although the fossil coverage in Australia is notably less extensive (temporally and geographically) than in Europe and North America. No synthesis of the fossil naticids of Australia has been written; Ladd (1977) and Majima (1989) included fossil records of several tropical species which are also found in Australia and named Australian fossil taxa were listed by Darragh (1970).

Superfamily TONNOIDEA

The Tonnoidea is a worldwide group of marine carnivores ranging from moderately small to very large (8–500 mm high). Their shells can be distinguished readily from members of related 'higher neotaenioglossan' superfamilies, such as Cypraeoidea and Naticoidea, by the prominently siphonate aperture, in many species produced into an anterior canal similar to that of some muricoidean neogastropods (for example, *Murex* species); much more prominent teleoconch sculpture; regular varices in many taxa; by the much more prominent periostracum; and by a much larger and more prominently sculptured protoconch, which in many taxa is composed primarily of conchiolin rather than calcium carbonate. The superficially similar, equally coarsely sculptured shells of some large, varicate muricoideans (particularly Muricinae) differ from those of tonnoideans by having the periostracum much less obvious and varices more numerous (never more than two per whorl in tonnoideans, compared with three to many per whorl in most muricoideans, although a few muricoideans such as *Eupleura* and *Aspella* have only two varices per whorl). Anatomically, tonnoideans are distinguished from closely related neotaenioglossans by their

pleurembolic proboscis, the presence of an undifferentiated mid-oesophageal gland, and the simple stomach which lacks a caecum or style. Most species have distinctive, enormously developed, complex salivary glands of two types, although they are smaller and of a single kind in Ficidae. Whereas the general appearance of the shell and the presence of a proboscis suggest affinities with the Muricoidea rather than with 'higher neotaenioglossans', the presence of a taenioglossan (rather than stenoglossan) radula and several anatomical features (such as passage of the salivary ducts through the nerve ring, rather than outside it) indicate that this resemblance is superficial, reflecting similar carnivorous life styles.

The eight families included here in the Tonnoidea are Bursidae, Cassidae, Ficidae, Laubierinidae, Personidae, Pisanianuridae, Ranellidae and Tonnidae. Warén & Bouchet (1990) noted that ficids are rather different from other tonnoideans and Riedel (1994) proposed splitting the Ficidae off in a separate superfamily, Ficoidea. In addition, Bandel & Riedel (1994) suggested placing the Laubierinidae in its own superfamily. Since this section was written an important review of the superfamily has appeared (Riedel 1995) to which the reader is referred for additional information. In this review, Riedel advocated reducing the Tonnidae to a subfamily of the Cassidae and the Bursidae to a subfamily of the Ranellidae. The superfamily name Tonnoidea is conserved under ICZN Article 40B (Ponder & Warén 1988, p. 302), but Cassoidea has been used by some workers (for example, Riedel 1994, 1995).

Some members of almost all families occur in Australia, and many are common, attractive, shallow-water marine shells. Approximately 135 species live around Australia; shells of most of the more common species have been illustrated in colour by Wilson & Gillett (1971), Hinton (1978), Wells & Bryce (1986) and Wilson (1993). The anatomy of several tonnoideans was described in detail and compared with that of other

caenogastropods by several early workers (for example, Haller 1893; Weber 1927). Other anatomical studies include those of Houbrick & Fretter (1969), Laxton (1969), Lewis (1972), Beu (1981), Warén & Bouchet (1990) and Riedel (1994). D'Asaro (1969) described in detail the development and organogenesis of two species.

Shells of Tonnoidea are highly varied in shape and sculpture, ranging from globose to subfusiform, pyriform and subtrigonal, with sculpture ranging from simple spiral cords to complex, intersecting, spiral and axial sculpture with prominent nodules at the intersections. Varices (ridges at former positions of thickened outer lips) are retained throughout growth in Ranellidae, Bursidae, Personidae, and a few tonnids and cassids; these all exhibit markedly episodic growth, the varices marking pauses in growth (Laxton 1970a, 1970b; Linsley & Javidpour 1980). No varices or any thickening of the outer lip are present in Ficidae, Laubierinidae, Pisanianuridae or most Tonnidae, and shells in these taxa seem to grow more or less continuously. Some genera traditionally placed in Tonnoidea because they bear prominent varices have been demonstrated to belong in Buccinidae (notably the genera related to *Colubraria*; Pilsbry & Vanatta 1904; Ponder 1968b; Beu & Maxwell 1987: appendix). A distinct anterior siphonal canal is present and is long, narrow, and prominent in many *Cymatium* species, but it is weakly defined in Laubierinidae and Pisanianuridae. A uniquely prominent posterior siphonal canal is present in Bursidae.

Although the shell apertures of many tonnoideans are complexly sculptured and personids, in particular, have a prominently ridged inner lip, all taxa that have spirally continuous columellar ridges and that were formerly included in Tonnoidea have been shown to belong in the Cancellariidae (Beu & Maxwell 1987).

Most tonnoideans have a thick, corneous operculum (the shape and nuclear position are taxonomically useful at subfamilial to generic levels) but adult Tonnidae and *Ficus* lack one. The head bears a pair of cephalic tentacles, with black eyes on swellings at their outer bases. In many shallow-water species, the tentacles are brightly striped with yellow or orange and dark brown to black, either along or around the tentacles. The proboscis is pleurembolic, and is short and wide in some taxa (notably *Tonna* species and bursids), presumably adapted for ingestion of whole prey (see for example, Houbrick & Fretter 1969), but is long, narrow and coiled within the proboscis sheath in some other taxa (observed in *Ficus* and *Distorsio* species; Lewis 1972; Beu 1981; Warén & Bouchet 1990). Jaw plates are paired and are large in most tonnoideans, composed of many rows of scales or platelets (Clench & Turner 1957; Warén & Bouchet 1990), but are small in the Personidae and greatly reduced (in *Tutufa*) or lost in the Bursidae. The radula is long, narrow, and taenioglossate (formula 2.1.1.1.2), with an equidimensional to wide central tooth bearing a major central cusp and few to many smaller denticles on each side; projecting basal triangular processes that interlock the column of central teeth are present in Tonnidae and Bursidae, and similar but much smaller processes are present in Pisanianuridae and Laubierinidae, but are absent in all other families. Lateral teeth are large, laterally elongate, interlocked and complexly cusped in most taxa, and all have long, narrow, strongly hooked marginal teeth. Many radulae have been illustrated, particularly well, by Bandel (1984) and Warén & Bouchet (1990). Mantle cavity organs present include a large ctenidium, a much smaller osphradium (bipectinate in most taxa, but monopectinate in Laubierinidae; Warén & Bouchet 1990), hypobranchial gland, rectum, and reproductive organs. The sexes are separate (except that *Laubierina* species may be protandrous hermaphrodites; see below) and males have a large, cylindrical to blade-shaped penis behind the right cephalic tentacle. The seminal groove is generally open, but is closed in some *Bursa* and *Tutufa* species (Bursidae; Houbrick & Fretter 1969; Beu 1981). A swollen pallial oviduct is present in females, but its detailed anatomy (Houbrick & Fretter 1969; Laxton 1969) has been investigated in very few species.

At least four significantly different types of egg masses are known in Tonnoidea (see review by Riedel 1995), but there are data about very few species. The capsule arrangement varies from single to hemispherical masses or long columns. The common New Zealand and southern Australian ranellid species, *Cabestana spengleri* and *Cymatium (Monoplex) parthenopeum*, are frequently found guarding their egg masses in the intertidal zone in summer; the whole mass resembles half an orange, as it is hemispherical with a thick, rough, multilayered outer structure surrounding the many closely packed, flat-topped capsules inside (figured by Laxton 1969, pl. 1A, B). An identical (although smaller) egg mass has been observed in *Bursa granularis* (A. Beu personal observations). The second type of egg mass consists of simple, randomly arranged, capsules attached to rocks. These may be parallel sided and flat topped, this type of mass having been reported in some bursids, the cassid *Cypraecassis testiculus* (Hughes, R.N. & Hughes 1987) and the ranellid *Ranella australasia* (Laxton 1969, pl. 2) and is possibly the common, primitive type in the superfamily. However, another simple type consists of single ovoid capsules attached to a narrow stalk and these are found in the primitive ranellid genus *Sassia* (Smith *et al.* 1989). The third type of egg mass is seen in some *Semicassis* species that lay tall, highly complex, spirally stacked egg masses quite different from those of any other gastropods (Abbott, R.T. 1968, pl. 1). In some of these species, high, irregular piles of spiral stacks are contributed to by numerous females (Abbott, R.T. 1968, pls 9, 10; Wilson & Gillett 1971, pl. 47).

Some bursids exhibit sexual dimorphism of apertural features. The apertural margin of males and non-breeding females is digitate. In egg-laying females the aperture becomes flared and the margin circular (observed in *Crossata californica* and in *Tutufa rubeta*; A. Beu personal observations). It seems likely that species showing this feature are those that produce complex, hemispherical egg masses, because the outer diameter of the egg mass matches that of the female shell aperture.

A few tonnoideans have direct development or only very short larval lives, but the great majority of species have long to extremely long planktotrophic larval lives, up to a year in some *Cymatium* species. A large literature now exists on the wide dispersal of larvae in many Ranellidae, Bursidae, Personidae and Tonnidae, and a few Cassidae (for example, Scheltema 1966, 1968, 1971, 1972, 1986a, 1986b, 1986c, 1988; Laursen 1981; Pechenik, Scheltema & Eyster 1984). It is not surprising, therefore, that many tonnoideans are among the most widely distributed of marine molluscs. Several species that are common in Australia are nearly cosmopolitan in warm seas. Other temperate species have circum-Southern Ocean ranges. D.T. Anderson (1959) studied the common eastern Australian ranellid *Cabestana spengleri* and reported direct development, but his tank conditions seem to have induced his larvae to settle and metamorphose on hatching. This species occurs on both sides of the Tasman Sea, and Laxton (1969) reported veliger larvae of this species in New Zealand; veligers have also been observed in material from Sydney, New South Wales (Riedel 1992).

Reviews of the superfamily and its classification have been provided by Thiele (1929–1935, as 'Stirps Doliacea'), Wenz (1938–1944), Beu (1981), Boss (1982) and, most usefully, Warén & Bouchet (1990). Overviews of the Ranellidae (as Cymatiidae) and Tonnidae have been provided by Kilias (1962, 1973). A catalogue of living species of Ranellidae, Bursidae and Personidae was published by Beu (1985), and most living Cassidae were revised by R.T. Abbott (1968), however, there have been no modern revisions of Indo-West Pacific species of *Ficus* or *Tonna*. Marshall (1992) revised the Recent species of the tonnid *Eudolium*. Warén & Bouchet (1990) added a remarkable range of new shell forms and reproductive behaviours to the Tonnoidea when they described the new families Laubierinidae and Pisanianuridae.

Some tonnoideans (particularly Cassidae and Ranellidae) have good fossil records in south-eastern Australia, as they have around much of the world. In particular, many *Sassia* species are recorded

from Eocene to Pliocene rocks in Australia. In contrast, only one tonnid, one *Ficus*, and no species of Bursidae, Pisanianuridae or Laubierinidae are known as fossils in Australia (although few fossil *Pisanianura* species and no fossil Laubierinidae are known worldwide). Outside Australia, most of the Australian genera (and several of the same species) have long fossil histories in Europe and North America. Many of the modern Indo-West Pacific species living in northern Australia are common in Miocene to Pleistocene rocks of Indonesia, the Philippines, and the Solomon Islands, but Indo-West Pacific Palaeogene fossils are distinct. The earliest tonnoideans are recorded from Late Cretaceous rocks of North America (Ranellidae; Beu 1988), Madagascar (Personidae; Beu 1988), and southern Africa (Ficidae; Wenz 1938–1944), and apparent Late Cretaceous Cassidae are known from Japan and far-eastern Russia (for example, Nagao 1932; Blank 1980) whereas Tonnidae and Bursidae have no fossil record before the Eocene. A Late Cretaceous radiation is inferred, and it is possible that such simple-shelled groups as Laubierinidae and Pisanianuridae (which somewhat resemble ‘lower taenioglossan’ superfamilies such as Cerithioidea) are specialised deep-water relicts, perhaps similar to the type of early Tonnoidea that gave rise to the other families.

Family Bursidae

The Bursidae (‘frog shells’) are a moderately diverse family with medium-sized to very large shells (the northern Indian Ocean *Tutufa bardeyi*, up to about 450 mm high and 300 mm wide, is one of the largest and most capacious of all gastropod shells). Twenty-two species are recorded from Australia. Nearly all live in the tropical north (a few extend into New South Wales or southern Western Australia) and nearly all are widespread outside Australia. Most occur throughout the Indo-West Pacific, but two are restricted to the Indian Ocean area, and one (*Bursa verrucosa*) lives only in New South Wales, northern New Zealand, and the Kermadec Islands. No species is restricted to Australia and there is no known fossil record of this family in Australia.

Bursids are identifiable by their thick, coarsely sculptured shells (Fig. 15.136A), which are heavily encrusted with coralline algae in most shallow-water species; the posterior exhalant siphon at the top of the outer lip; the periostracum calcified, producing a chalky intritacalx, in shallow-water taxa; a third accessory salivary gland, additional to the two seen in some other Tonnoidea (Fig. 15.136D; Beu 1981); absence of jaw plates, except for minute remnants in *Tutufa* (Beu 1981); and a relatively small, narrow, triangular central radular tooth bearing prominent basal interlocking processes (Fig. 15.136E–G). The varices in most taxa are aligned up the spire sides (about 180°–200° apart, a growth increment of half a whorl, as in the ranelline ranellids), but in *Tutufa* are 240° apart (a growth increment of two-thirds of a whorl). A few *Bursa* and *Bufonaria* species have varices aligned towards the apical region of the shell, but diverging towards the aperture. The protoconch is multispiral and broadly conical, often with reticulate sculpture on the early whorls (Fig. 15.136B). The position of the nucleus of the operculum is diagnostic for genera: anteriorly terminal in *Bursa*; subcentral to subterminal near the right edge in *Tutufa* (resembling that of the ranellid *Charonia*); and in the centre of the left (columellar) margin in *Bufonaria* (forming a fan-shaped operculum resembling that of the phaliine Cassidae).

Bursa species are intertidal to subtidal epifaunal carnivores. They are common on coral reefs and also on rocks. Little is known of the details of bursid feeding or reproduction. Egg capsule form is described under the superfamily. Species of *Bufonaria* and *Tutufa* and the taller, thinner-shelled *Bursa* species are dredged or trawled on the continental shelf. Houbbrick & Fretter (1969) described the head-foot anatomy, feeding and reproductive system of Hawaiian *Bursa rhodostoma*, *B. granularis* and *B. cruentata* (Fig. 15.136C); all three species also occur in northern Australia. Gross anatomy was illustrated by Beu (1981, figs 6–8) for *Bursa ranelloides*, *Tutufa bufo* and *T. rubeta* as well as stomach morphology of these and some other tonnoideans (Fig. 15.136D;

Beu 1981). Houbbrick & Fretter (1969) described feeding in *Bursa* in some detail: all three species studied removed polychaetes and sipunculids from their tubes or from crevices and ingested them whole; the radula served to pack the worm into the proboscis. The strongly acid saliva inactivates polychaetes, and so aids capture. Ingestion of one worm took from 90 seconds to 2.5 minutes and digestion of the body wall followed rapidly.

Family Cassidae

Cassids (‘helmet shells’) are recognised by their solid, globose shells with a moderate to low spire and very large, enveloping last whorl; prominently thickened and reflected outer lip (remaining as varices on shells of several taxa, notably *Cassis* and *Phalium* – hence growth is episodic); a strongly thickened, smooth to complexly sculptured, flared collar over the inner lip and much of the previous whorl in many taxa; anterior siphonal canal short and narrow, and, in many taxa, strongly twisted (Fig. 15.137A–C). Teleoconch exterior sculpture is relatively weak, and dominantly spiral in most taxa. The periostracum is thin and inconspicuous in most members, and most have a bright banded or spotted colour pattern on the shell exterior (Pl. 27.3). The central radular tooth (Fig. 15.137I, J) lacks the interlocking process of tonnids and bursids, and all adults have an operculum.

Many taxa occur in quite shallow water (particularly species of *Cassis*, *Casmaria*, *Cypraecassis*, *Phalium* and *Semicassis*), a few even intertidally, where most are found on sand (a few prefer rocky substrata). All cassids in which feeding has been investigated are predators of echinoids (Fig. 15.137E, F), producing an acid secretion that removes the spines from an area of the echinoid test before either penetrating the anus or drilling a hole through the test using their modified feeding apparatus (Fig. 15.137F, G, H; Abbott, R.T. 1968 and many references cited therein; Hughes, R.N. & Hughes 1971; Wilson & Gillett 1971). R.N. Hughes & Hughes (1981) gave a particularly full and valuable account of feeding in *Cassis* and *Cypraecassis*, with a collation of published accounts of feeding in the Cassidae.

Australian cassid species were revised by Iredale (1927) and R.T. Abbott (1968), but subsequent study of the larger collections now available has led to the recognition of fewer, more variable species, and of a different generic classification arranged in two subfamilies, Cassinae and Phaliinae (Beu 1981). The genera *Morum* and *Oniscidia*, formerly included in the Cassidae, have been shown to belong to the neogastropod family Harpidae (Hughes, R.N. 1986).

Two subfamilies are recognised currently, the Cassinae and Phaliinae. The Cassinae includes most of the larger and more brightly coloured cassids; particularly well known are the large tropical species *Cassis cornuta* (to ca 350 mm high) and *Cypraecassis rufa*. The latter is of economic importance as the resource material for cameos, and *Cassis cornuta* (Fig. 15.137A) is used extensively as an ornament. The diagnostic characteristic of the subfamily is the oval operculum with a subcentral to nearly anterior terminal nucleus. Also, almost all taxa have a straight or only weakly twisted anterior siphonal canal, contrasting with the very strongly twisted, dorsally directed canal (separated only narrowly from the last whorl) of Phaliinae. The only exception is *Cypraecassis*, placed in Cassinae because of its oval operculum with subcentral nucleus (Abbott, R.T. 1968, pl. 44) and its close resemblance to *Cassis*, but having the strongly twisted, fasciolate canal otherwise restricted to Phaliinae. Some *Galeodea* species have a twisted, dorsally directed siphonal canal also, but in *Galeodea* the twisting is less marked and the canal longer than in Phaliinae, resulting in a canal that is much less obviously notched and fasciolate and markedly more widely separated from the last whorl than in Phaliinae. Information on the anatomy of the relatively generalised (primitive?) cassine genus, *Galeodea*, is provided by Reynell (1905), and of the Australian *G. maccamleyi* by Ponder (1983d). Radular and anatomical comparisons between *Cassis*, *Galeodea*, and the small, simply sculptured, deep-water genera related to *Oocorys* (including *Dalium* and *Hadroocorys*;

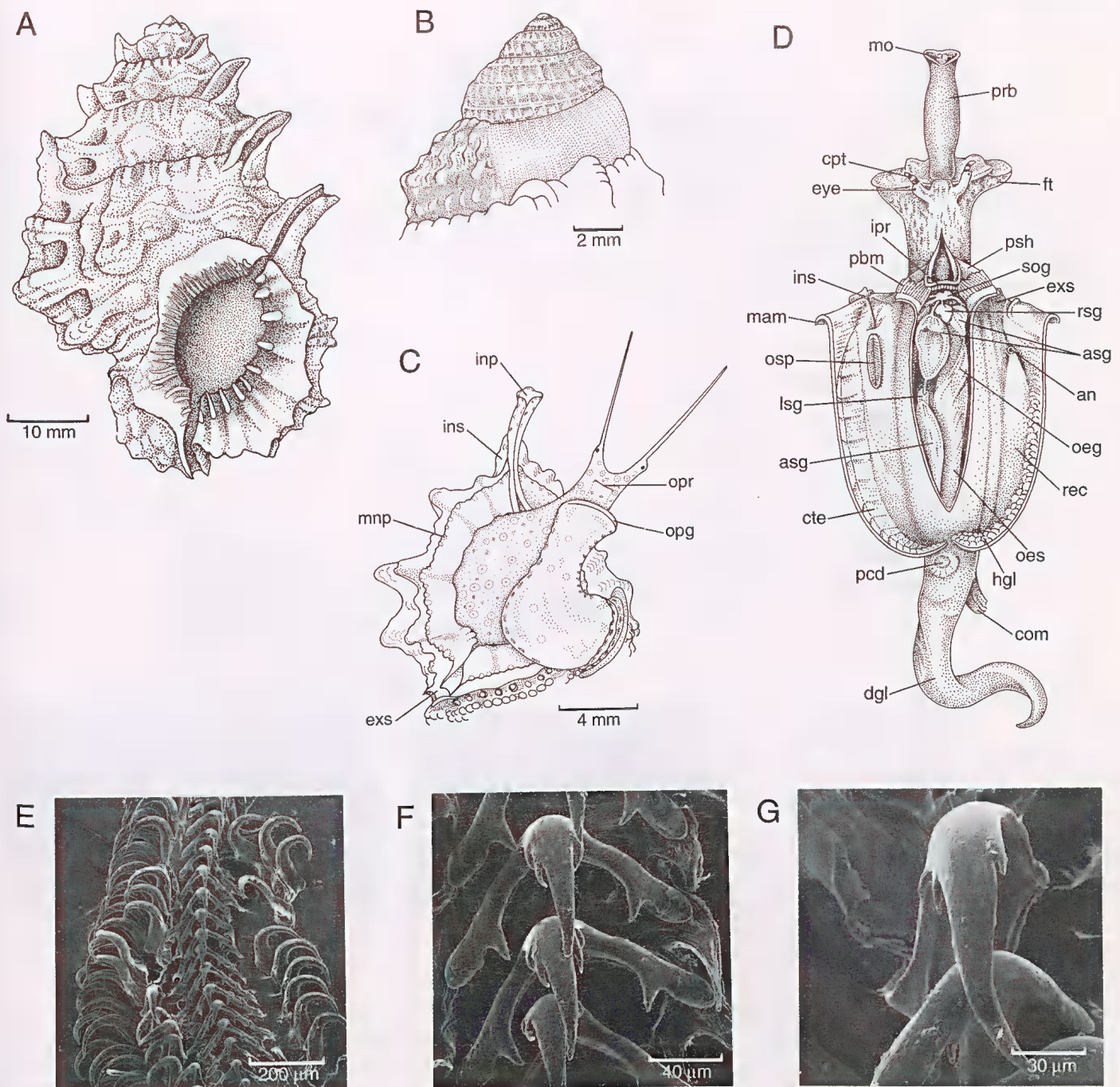


Figure 15.136 Family Bursidae. **A**, *Bursa lamarckii*, shell, apertural view. **B**, *Bursa latitudo*, protoconch. **C**, *Bursa cruentata*, animal extended from its shell, ventral view. **D**, *Tutufa rubeta*, gross anatomy of mantle and cephalic cavities. **E–G**, *Tutufa oyamai*, radula: **E**, portion of radula ribbon with lateral and marginal teeth parted to show central tooth; **F**, detail of central tooth; **G**, lateral tooth, turned half outwards to show denticles on base of main cusp. **an**, anus; **asg**, accessory salivary gland; **com**, columellar muscle; **cpt**, cephalic tentacle; **cte**, ctenidium; **dgl**, digestive gland; **exs**, exhalant siphon; **eye**, eye; **ft**, foot; **hgl**, hypobranchial gland; **inp**, inhalant pallial siphon; **ins**, inhalant siphonal canal; **ipr**, base of inverted proboscis; **lsg**, left salivary gland; **mae**, mantle edge; **mnp**, papillae on edge of mantle; **mo**, mouth; **oeg**, oesophageal gland; **oes**, oesophagus; **opr**, opening of proboscis sheath; **osp**, osphradium; **pbm**, proboscis retractor muscles; **pcd**, pericardium; **prb**, proboscis; **psh**, proboscis sheath; **rec**, rectum; **rsg**, right salivary gland; **sog**, supra-oesophageal ganglion. (**B**, after Beu in press; **C**, after Houbrick & Fretter 1969; **D**, after Beu 1981; **E–G**, from Beu 1981)

Quinn 1980) have shown no significant differences, and their shell and opercular features are similar. In particular, the operculum of *Galeodea maccamleyi* figured by Ponder (1983d, pl. 2), is identical to that of *Oocorys*. The genera previously placed in a 'family' Oocorythidae now seem best included in Cassinae (see also Warén & Bouchet 1990). Six cassine species are known from Australia, four in *Cassis*, one in *Cypraecassis* and one in *Galeodea*. *Cassis* has a good fossil record in Miocene rocks of southern Australia. *Oocorys* has not been recorded from Australia, but *O. sulcata*, originally described from the Atlantic (Turner 1948), is common at depths of 1000 m or more off South Africa (R. Kilburn personal communication) and around New Zealand, and will almost certainly be found around Australia.

The Phaliinae include the smaller and more evenly globose 'helmet shells', from the tropical Indo-West Pacific *Casmaria*, *Phalium* and *Semicassis* species, to the common shallow-water *Semicassis* species of New Zealand and southern Australia (formerly included in the synonyms *Xenophalium* and *Xenogalea* of Iredale, 1927). Four species of *Phalium* (elongate shells with axial as well as spiral sculpture, retaining all varices down the spire) and 12 of *Semicassis* (more globular, smoother shells with dominantly spiral sculpture, and only a terminal varix) are recorded from Australia, as well as three species of *Casmaria* and at least one of the nodulose, offshore genus, *Echinophoria*. Diagnostic subfamilial characters are the short, strongly dorsally twisted, narrowly constricted siphonal canal, forming a siphonal

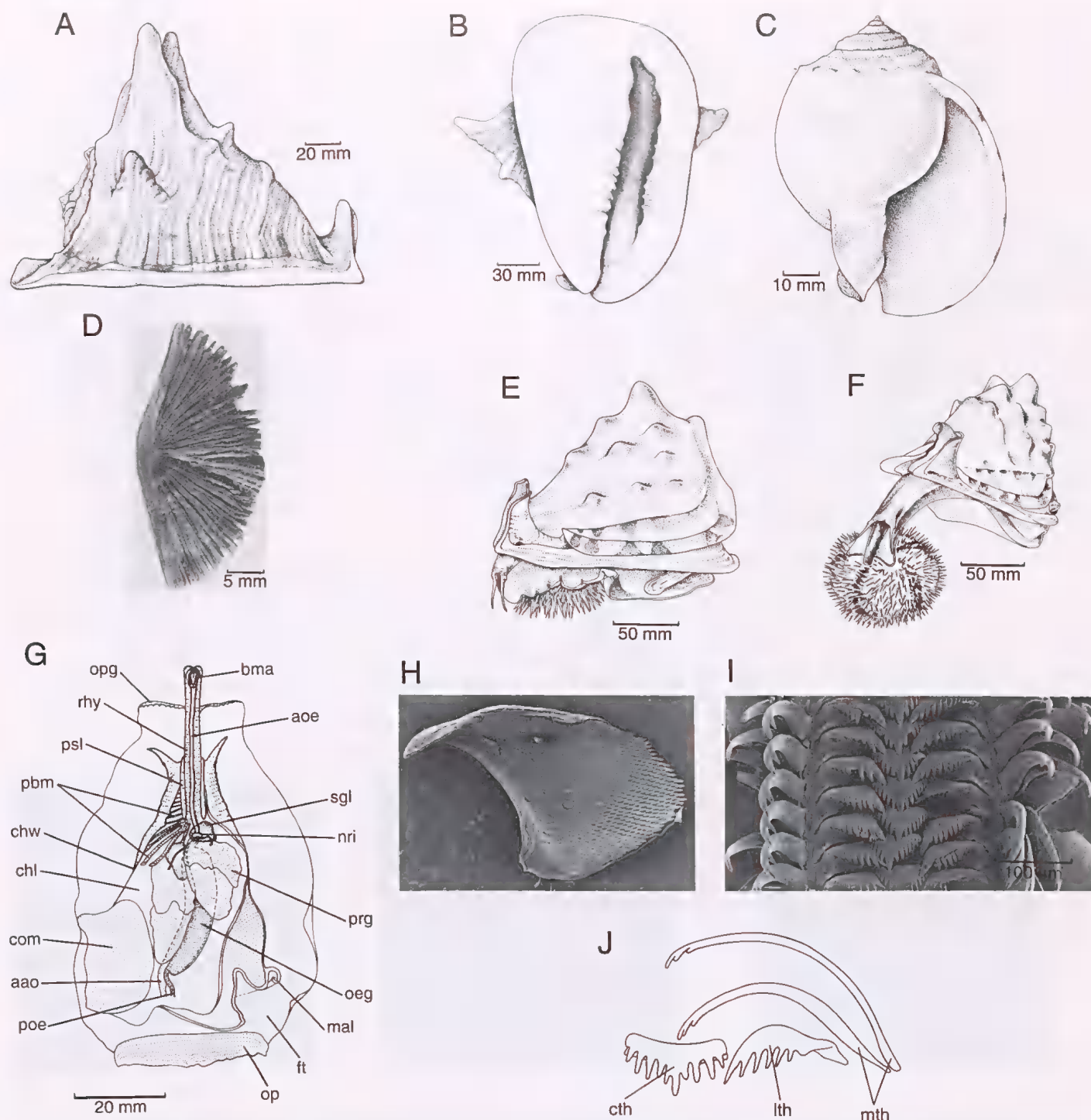


Figure 15.137 Family Cassidae. *Cassis cornuta*, shell: A, lateral view; B, apertural view. C, *Semicassis pyrum*, shell, apertural view. D, *Semicassis granulatum*, operculum, outer surface. E, F, *Cassis tuberosa*, feeding: E, *C. tuberosa* arching over the sea urchin, *Tripneustes ventricosus*, in the initial phase of attack; F, urchin grasped by front part of foot. G, *Cassis tuberosa*, feeding apparatus and associated glands. H, *Galeodea maccamleyi*, jaw. I, *Galeodea maccamleyi*, portion of radular ribbon. J, *Cassis cornuta*, half a transverse row of radular teeth. aao, anterior aorta; aoe, anterior oesophagus; bma, buccal mass; chl, cephalic haemocoel; chw, cephalic haemocoel wall; com, columellar muscle; cth, central tooth; ft, foot; lth, lateral tooth; mal, cut mantle; mth, marginal teeth; nri, nerve ring; oeg, oesophageal gland; op, operculum; opg, opening of pedal gland; pbm, proboscis retractor muscles; poe, posterior oesophagus; prg, proboscis gland; psl, proboscis sheath lumen; rhy, rhynchodaeum; sgl, salivary gland. (D, from Warén & Bouchet 1990; E–G, Hughes, R.N. & Hughes 1981; J, after Thiele 1929–1935)

[A–C, S. Weidland; E, F, R. Plant; G, J, I. Hallam; H, I, W.F. Ponder]

fasciole, and the fan-shaped operculum (Fig. 15.137D) with its nucleus at the junction of two straight edges on the columellar margin (as in the bursid genus *Bufonaria*). The operculum bears prominent radial ridges and grooves in many species (particularly *Semicassis* species with relatively strong spiral sculpture) but is smooth or weakly commarginally ridged in others. Some species are found over much of the Indo-West Pacific and occur in northern Australia (*Phalium*, *Casmaria* and *Echinophoria* species, and some *Semicassis* species such as *S. bisulcata*). Others are temperate circum-Southern Ocean species, and occur in southern Australia (notably *Semicassis labiata*). *Semicassis pyrum*, in particular, washes ashore commonly on sand beaches throughout New Zealand, but is less common in southern Australia. It occurs

in shallow water, although specimens are also commonly dredged on soft substrata down to at least 100 m. *Semicassis labiata* is reasonably common in New South Wales, and often occurs intertidally; evidently it feeds on sand-inhabiting echinoids such as clypeasteroids and spatangoids. Little has been documented of phalline ecology, feeding, or reproduction. The egg masses are described above in the superfamily description. The wide distributions of many species (particularly the circum-Southern Ocean *S. labiata*) are indicative of extended planktotrophic larval life; Laursen (1981) and Warén & Bouchet (1990) have recorded planktonic larvae of *Semicassis* and *Cypraecassis* species from the Atlantic Ocean. Some other taxa with limited distributions around Australia have a calcareous paucispiral protoconch, suggestive of

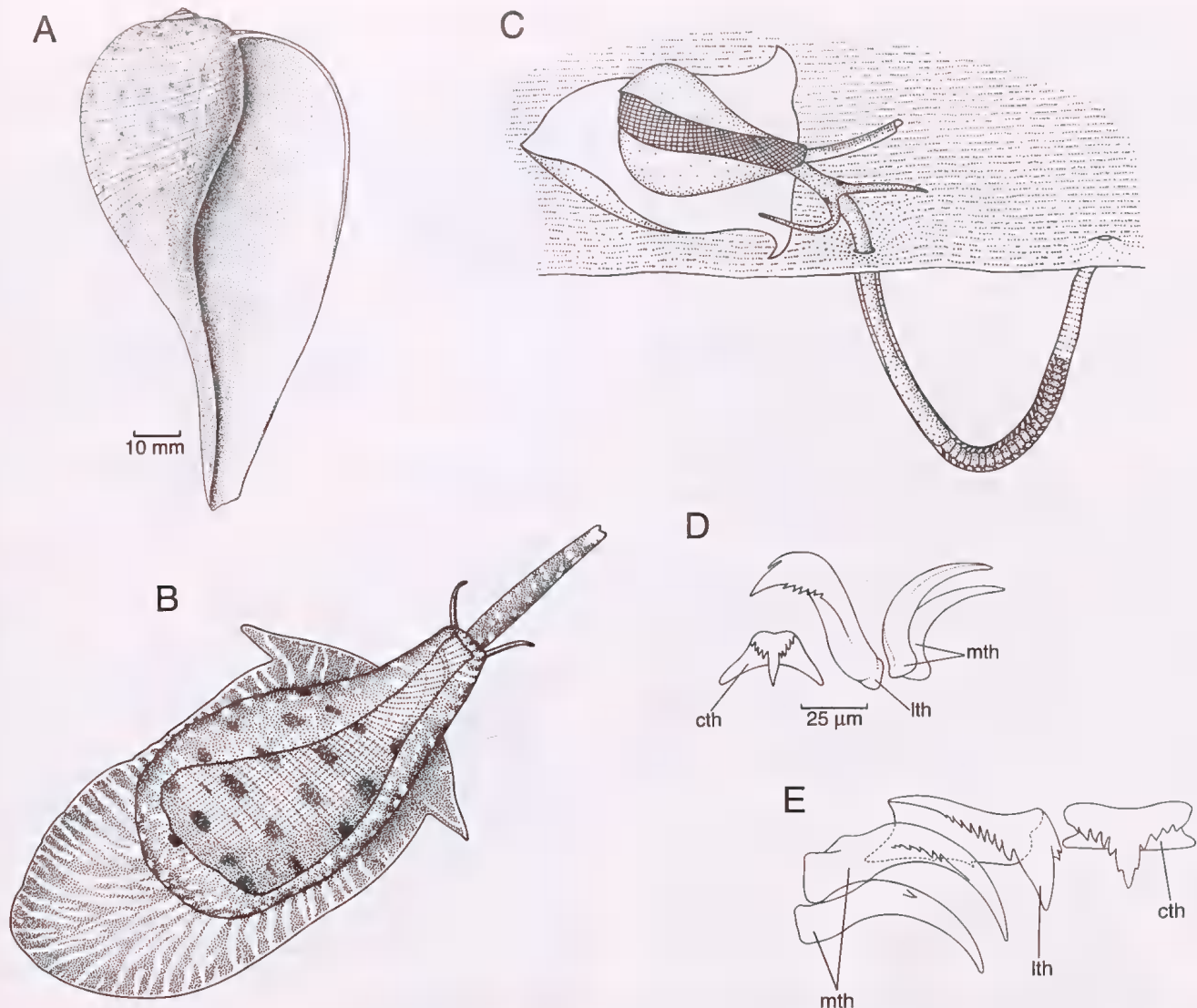


Figure 15.138 Family Ficidae. A, *Ficus subintermedia*, shell, apertural view. B, *Ficus eosyla*, crawling with proboscis extended. C, hypothesised feeding strategy of *Ficus* species; the mantle for the most part is covering the shell, and the proboscis is extruded to suck in a polychaete. D, E, two half transverse rows of radular teeth: D, *Thalassocyron bonus*; E, *Ficus reticulata*. cth, central tooth; lth, lateral tooth; mth, marginal teeth. (B, after photograph in Wilson 1993; C, D, after Riedel 1994; E, after Thiele 1929–1935) [A, S. Weidland; B, C, Eadie; C–E, I. Hallam]

direct development (*Cassis fimbriata*, *C. nana*; Abbott, R.T. 1968). Beu (1976a) pointed out that *S. pyrum* and several other tonnoideans (most are Ranellidae) have no fossil record in the Southern Ocean until Pleistocene time, but have close relatives (or, for the ranellids, apparently the same species) in Miocene and Pliocene rocks of the Europe–Mediterranean area. This history also implies transport through the South Atlantic and around the Southern Ocean as long-lived planktotrophic larvae, perhaps enabled to cross the tropical barriers by cooling during glaciations. By contrast, *Echinophoria* has a good fossil record in Australia and New Zealand.

Family Ficidae

The Ficidae ('fig shells') are a small family (four species known from Australia, perhaps 10 to 12 in the world fauna) represented now by only two genera, *Ficus* and *Thalassocyron*. *Ficus* species have the shell fig-shaped, elongate and graceful, with a very low to almost flat spire, and a large, enveloping last whorl drawn out into a long, widely open anterior canal (Fig. 15.138A). Shell sculpture is fine, and predominantly spiral, although many species also have fine intersecting axial riblets. The aperture is simple, the outer lip thin, the inner lip smooth and narrow. Shell growth is apparently continuous. The protoconch is unusual for Tonnoidea in having an initial smooth stage (varying from one to three whorls) and a subsequent 0.2 to 2 whorls bearing fine cancellate sculpture. The salivary glands are also unusual for Tonnoidea in being relatively small and simple (Warén & Bouchet 1990), so

Ficus evidently feeds differently from other tonnoideans, and does not require acidic salivary secretions to inactivate or help penetrate its prey. Ficids apparently feed on polychaetes and perhaps other 'worms' (Riedel 1994). Wilson & Gillett (1971) reported that *Ficus* feeds on 'sea urchins and other echinoderms', but evidently this is not so. The proboscis is narrow and extremely long (Fig. 15.138B), but extensively coiled in the proboscis sheath at rest, and has a very small buccal mass, so suctorial feeding or ingestion of small tubicolous animals seem likely (Fig. 15.138C). *Ficus* species lack an operculum, although a black, irregularly circular, very small one is present in *Thalassocyron*. The animal of *Ficus subintermedia* (Wilson & Gillett 1971, frontispiece) is attractive, dark pink with small, irregular cream spots, and is distinctive in having a widely expanded, thin foot with antero-lateral pointed extensions (as in *Tonna*), and in having mantle lobes covering much of the shell when the animal is expanded (Fig. 15.138B), a character not reported for any other tonnoidean. Arakawa & Hayashi (1972) demonstrated sexual dimorphism in *Ficus subintermedia*, the most common Australian ficid, both shells and creeping animals differing in shape. In particular, the antero-lateral foot projections are narrower and more backwardly directed in males than in females. Flattened egg capsules are laid in a long row (Riedel 1994). Like the other relatively smooth-shelled tonnoideans (Tonnididae, most Cassidae, a few *Cymatium* species), *Ficus* species evidently spend much of the time moving, partly to almost completely, buried in sand. Most specimens are trawled on the continental shelf at relatively shallow depths.

15. PROSOBRANCHS

The other extant genus that has usually been referred to the Ficidae is *Thalassocyon*, which contains only one species, *T. bonus* (Warén & Bouchet 1990). This species differs from *Ficus* in having a row of large, compressed spines around the periphery (forming a prominent shoulder angle); in its much more obvious, velvety periostracum; and in retaining a small, black operculum in adults (much smaller than the aperture). A new family, Thalassocyonidae, has recently been proposed for this genus (Riedel 1994). Both genera have a radula with a relatively small, triangular central tooth but large, laterally elongate, strongly cuspidate lateral teeth (Fig. 15.138D, E; Beu 1969; Warén & Bouchet 1990).

The family has a long fossil history. The earliest putative member is *Protopirula capensis* (Late Cretaceous, South Africa; Wenz 1938–1944). An early Cainozoic radiation produced several nodulous to spinose genera and it appears likely that *Thalassocyon* is descended from one of these early Cainozoic strongly sculptured genera, such as *Priscoficus*. One fossil species of *Ficus*, *F. altispira* occurs in Australian Early Miocene rocks, and several species of *Priscoficus* and *Ficus* occur in Palaeocene to Middle Miocene rocks in New Zealand.

Three of the *Ficus* species found in northern Australia range widely throughout the tropical Indo-West Pacific, and presumably have planktotrophic larvae. The fourth, *F. tessellata*, is endemic to Western Australia. *Ficus tessellata* has a dome-shaped protoconch of one whorl, and evidently has direct development. *Thalassocyon bonus* is known from 1000–3000 m off South Africa, Amsterdam Island, eastern Australia, north-eastern New Zealand and the Kermadec Trench (Warén & Bouchet 1990) and evidently has a planktotrophic larva.

Family Laubierinidae

Laubierinids are clearly distinguished from other Tonnoidea by the monopectinate osphradium. They are so distinct from other tonnoideans that Bandel & Riedel (1994) proposed that they be removed from the superfamily. Both laubierinid genera are recorded from Australia. *Akibumia* (formerly referred to Trichotropidae) has a thin, inflated, low-spired, near-turbiniform shell (Fig. 15.139A, B; weakly sculptured with spiral threads in *A. flexibilis* and *A. schepmani*, but with three prominent spiral cords angling the shell surface in *A. orientalis*); a typically tonnoidean cancellate planktonic larval shell; and a typically tonnoidean radula with a long, narrowly pointed main cusp on the central tooth, very similar to radulae of *Tonna*, *Eudolium*, *Galeodea*, and *Pisanianura* (Warén & Bouchet 1990). The known *Akibumia* specimens are 15–18 mm in diameter. In Australia, *A. orientalis* is recorded from one specimen collected off Sydney in 1106–1143 m, and *A. schepmani* is recorded from one specimen taken off the Gold Coast, Queensland, in 550 m (Warén & Bouchet 1990).

The genus *Laubierina* differs from *Akibumia* in having a more ficid-like, medially angled shell, but the anterior canal is a similarly short, open notch in both genera. The protoconch and radula of *Laubierina* closely resemble those of *Akibumia* (Fig. 15.139A, B). The single known adult specimen of *L. peregrinator* is 18.8 mm high and 19.5 mm in diameter. *Laubierina* is highly distinctive in displaying protandrous hermaphroditism; one of the newly metamorphosed larvae investigated by Warén & Bouchet (1990) was a sexually mature male, with a large penis, a well-developed sperm groove, and a testis packed with sperm; the two known live-collected adults were female. Protandrous hermaphroditism seems a logical strategy for rare species in the deep sea.

Laubierina is recorded from Australia on the basis of a single specifically indeterminable larval shell, from off Broken Bay, New South Wales, in 1000 m (Warén & Bouchet 1990).

Family Personidae

This small family was separated recently from the Ranellidae by Beu (1988) on the grounds that it has had a separate history since Late Cretaceous time, and its anatomical features (including the form of the proboscis, radula and operculum) are more like those of Ficidae than of Ranellidae.

The shell of *Distorsio*, the major personid genus and the only one so far reported from Australia, is remarkable for its asymmetrical coiling, which becomes more pronounced as the shell grows (Fig. 15.140A). At each growth pause the animal secretes a prominent toothed ridge at the base of the columella, protruding strongly into the aperture, and a slightly flared and widely inward-thickened, strongly toothed outer lip. In all, this produces a unique, heavily 'armoured' aperture that presumably protects the animal from predators. Apertural features are retained as the shell grows, and the irregular coiling (brought about by expansion of the whorl between growth pauses) appears to result from the necessity to accommodate the retracted head-foot in a diameter greater than that of the aperture. Ackerly (1989) analysed the coiling of *Distorsio reticularis* (which is common throughout the Indo-West Pacific, including northern and eastern Australia) stereographically and showed that an initially regular juvenile form is followed by angular shifts of the coiling axis of 4° to 7°, increasing as the shell grows. More distorted species such as the common *D. anus* appear to shift their axis of coiling much more markedly. As in the ranellid subfamily Cymatiinae and in those cassids that retain regular varices at growth pauses (principally *Cassis* and *Phalium*), growth increments in personids occupy two thirds of a whorl, i.e. varices are situated every 240° around the coiling axis. The shell surface is crisply sculptured with cancellate axial ridges and narrow spiral cords and almost all species develop a wide inner lip shield, masking the sculpture of the previous whorl, at each growth pause.

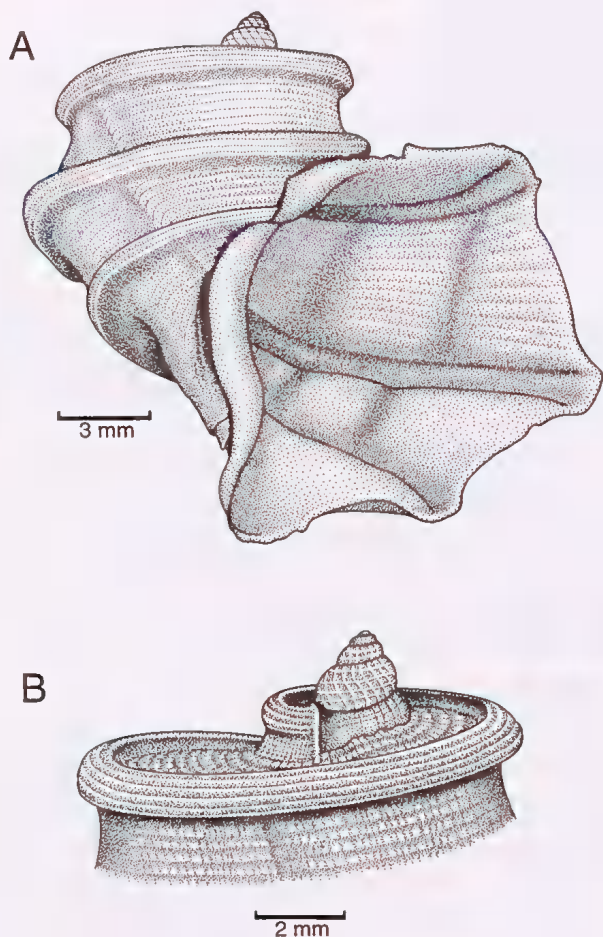


Figure 15.139 Family Laubierinidae. *Akibumia orientalis*, collected from deep water off Sydney, New South Wales. A, B, shell: A, apertural view; B, first few whorls showing protoconch. [C. Eadie]

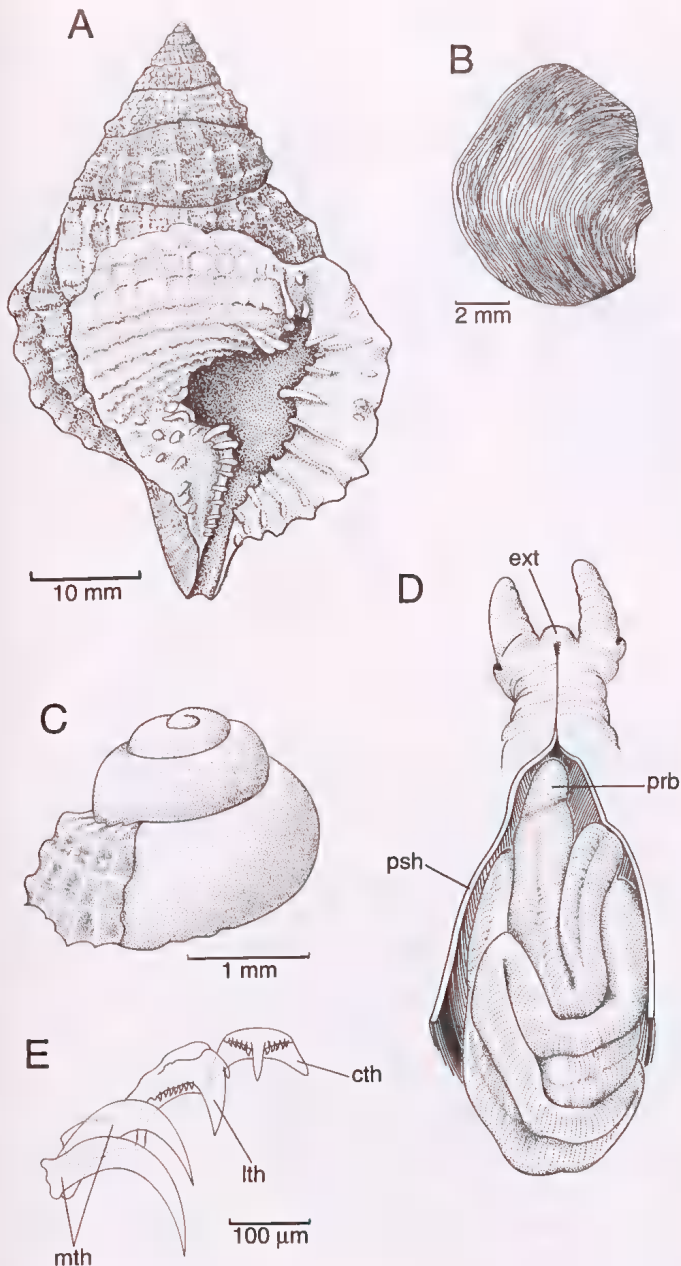


Figure 15.140 Family Personidae. A, *Distorsio reticularis*, shell, apertural view. B–E, *Distorsio perdistorta*: B, operculum, outer surface; C, protoconch; D, proboscis sheath opened dorsally to show the fully retracted proboscis; E, half a transverse row of radular teeth. cth, central tooth; ext, exit of proboscis sheath; lth, lateral tooth; mth, marginal teeth; prb, proboscis fully retracted; psh, proboscis sheath opened dorsally. (B–E, after Lewis 1972)

[A, S. Weidland; B–E, I. Hallam]

The anatomy of *Distorsio* species resembles that of *Ficus*. A long, narrow proboscis is coiled extensively in the proboscis sheath when at rest (Fig. 15.140D), and the buccal mass is small. The operculum (Fig. 15.140B) is small, subcircular, black in most species, and irregularly circular in many specimens (Clench & Turner 1957); it closely resembles that of *Thalassocyron*. The radula (Fig. 15.140E) is similar to that of *Ficus* species in most features, but the central tooth is distinctive in having down-curved outer corners (Lewis 1972; Beu 1978; Warén & Bouchet 1990). The jaw plates are unique to the family, being small, narrow, strongly curved, and having only a few rows of scales (Lewis 1972).

Although little is known of personid ecology and reproduction, the wide distributions of species indicate that most have planktotrophic larvae. Laursen (1981, figs 42, 43; pl. 2, fig. 6a, b) figured larval shells from the Atlantic plankton bearing highly distinctive, very large, periostracal spines in three to four spiral rows.

The living members of the family were reviewed recently by Kronenberg (1994). Five species of *Distorsio* have been collected around northern Australia and the distribution of the most common species, *D. reticularis*, ranges to New South Wales and southern Western Australia. The smallest living tonnoidean, '*Personopsis*' *pusilla* (8–15 mm high), occurs throughout the Western Pacific from Japan and Hawaii to New Caledonia and a few specimens are known from northern Australia.

The earliest known fossil is a typical *Distorsio* from Late Cretaceous rocks of Madagascar. A distinctive genus occurs in Palaeocene rocks at the Chatham Islands (east of New Zealand), and *Distorsio* and *Personopsis* are well represented in Oligocene and Neogene rocks of Europe, eastern North America, and the tropical Pacific. One fossil species, *D. interposita*, occurs in Oligocene rocks at Torquay, near Melbourne, Victoria.

Family Pisanianuridae

Pisanianura, the only genus in the family Pisanianuridae, has a relatively simple, weakly sculptured, bucciniform shell without varices and with the outer lip only lightly thickened (Fig. 15.141A–C); a typically tonnoidean, cancellate, planktotrophic larval shell; and a typically tonnoidean radula (Fig. 15.141E) resembling those of Ranellidae, Cassidae and, in particular, of *Laubierina* (Warén & Bouchet 1990). Features distinguishing *Pisanianura* species from the Ranellidae are the apparently continuous shell growth (such as lack of varices or other evidence of episodic growth) and the weakly defined anterior siphonal canal, which is formed largely by the unique curved, 'cut away' columellar base, and thus resembles those of such cerithioideans as *Bittium* and *Campanile*. The radula form (with minute projections on the lower margin of the central tooth), the simple aperture with a weakly defined anterior canal, and the continuous growth suggest that the closest relationship of *Pisanianura* may be with the Laubierinidae, but *Laubierina* and *Akibumia* have a monopectinate rather than a bipectinate osphradium.

This family (elevated from a subfamily of Ranellidae; Warén & Bouchet 1990), until 1990 was included in the Buccinidae. At present, the true relationships must remain speculative, and *Pisanianura* seems best segregated in a family of its own. *Pisanianura* and Laubierinidae are probably distinct groups of tonnoideans that independently became specialised for life in the deep sea. Figure 15.141D, showing features of internal anatomy, allows comparisons between families.

Both living *Pisanianura* species are very widespread and both have been found in Australia and New Caledonia. *Pisanianura breviaxis* (adult shells up to 46 mm high) occurs widely in the western Pacific from Japan to off northern New Zealand, and *P. grimaldii* (up to 27 mm high) occurs in the Atlantic and Indian Oceans as well as the western Pacific (Warén & Bouchet 1990). The genus has a fossil record from the Miocene in both Europe and New Zealand.

Family Ranellidae

The Ranellidae ('triton shells'), long known as the Cymatiidae, are much the most diverse family in the Tonnoidea (56 species in nine genera known in Australia) and exhibit a correspondingly large variety of shell forms and sculpture (Fig. 15.142A–D), ecological preferences, and geographic ranges. The family is divided into two subfamilies: Ranellinae and Cymatiinae. A classification and catalogue of the living species (and of Personidae and Bursidae) was given by Beu (1985).

Ranellid shells range in length from 15 mm to nearly 500 mm (*Charonia tritonis*, Fig. 15.142I, is one of the largest gastropods) and most species are subfusiform to subtriangular in shape. Most are moderately large intertidal to shelf epifaunal carnivores and are found on rocky shore, coral reef, or sand habitats, and many are predators of echinoderms (mostly asteroids or echinoids) or

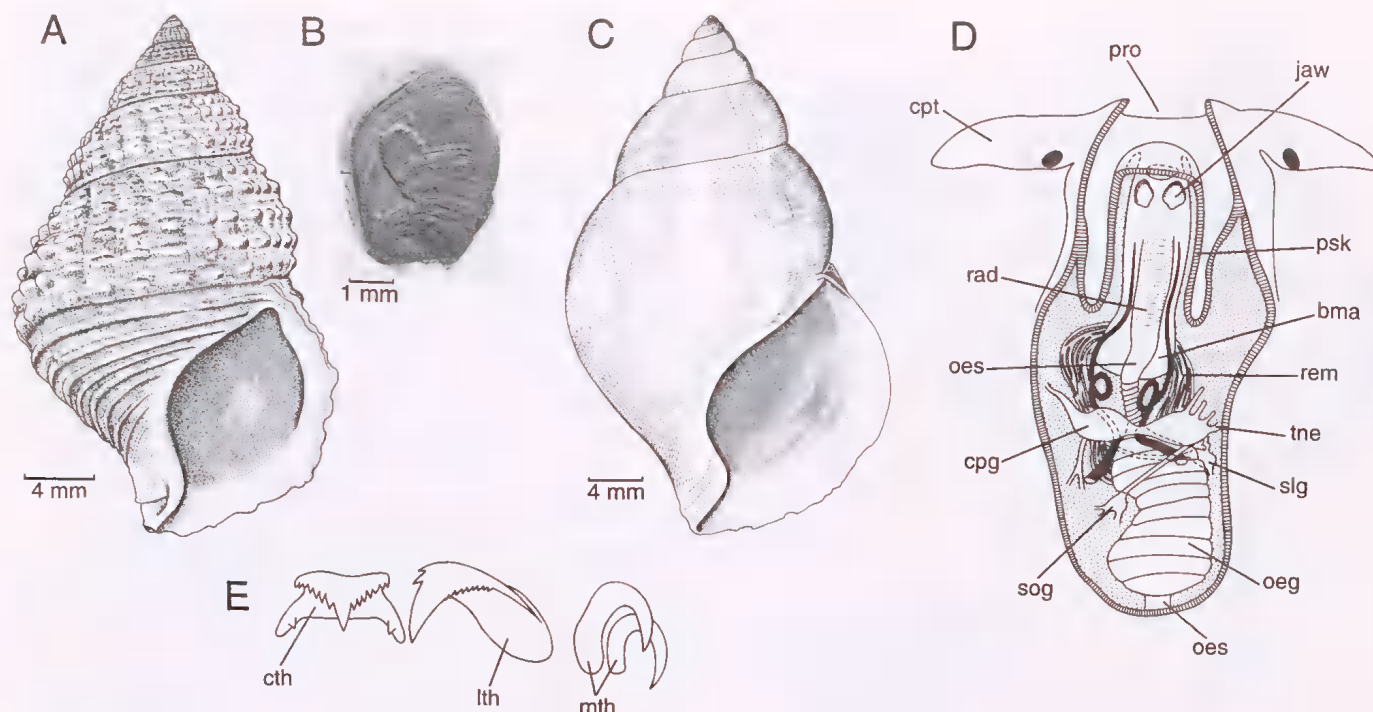


Figure 15.141 Family Pisanianuridae. A, B, *Pisanianura grimaldii*: A, shell, apertural view; B, operculum, outer surface. C, *Pisanianura brevixaxis*, shell, apertural view. D, *Pisanianura brevixaxis*, schematic plan of body cavity, salivary glands have been removed. E, *Pisanianura grimaldii*, half a transverse row of radular teeth. bma, buccal mass; cpg, cerebropleural ganglion; cpt, cephalic tentacle; cth, central tooth; jaw, jaw; lth, lateral tooth; mth, marginal teeth; oeg, oesophageal gland; oes, oesophagus; pro, proboscis opening; psk, proboscis skirt; rad, radula; rem, retractor muscles; slg, suboesophageal ganglion; sog, supra-oesophageal ganglion; tne, tentacle nerve. (B, D, Warén & Bouchet 1990; E, Riedel 1995)

tunicates. In contrast to the semi-infaunal, smooth-shelled members of the Cassidae, Ficidae and Tonnidae, most ranellids resemble the similarly epifaunal Bursidae and Personidae in having prominent exterior teleoconch sculpture, with nodules at spiral and axial sculptural intersections. A distinctive character of the family is its prominent, thick, brown, bristled and bladed to velvet-like periostracum (giving rise to the common name of 'hairy tritons' for some species of *Cymatium*). The radula has a rather generalised tonnoidean form (Fig. 15.143D–F), with an equi-dimensional central tooth having few cusps in the most primitive genus, *Sassia*, and in *Cabestana* and all Ranellinae, but with a much wider, multicuspidate central tooth in the more highly derived genera of Cymatiinae, *Charonia* and *Cymatium*. Specialised interlocking projections of the bases of the central teeth in the Bursidae and Tonnidae have not been observed in any ranellid radulae. Features of the digestive system and female reproductive system are illustrated in Figure 15.143A, B, respectively, and the hemispherical egg mass in Figure 15.143C.

This family contains some of the most widely distributed of molluscs with teleplanic larvae, and most taxa have primarily conchiolin protoconchs (Fig. 15.142E–G). Many have larvae that feed in the plankton and are able to postpone metamorphosis until they reach a substratum suitable for settling (see for example, Scheltema 1966, 1971, 1986a, 1988; Pechenik *et al.* 1984; protoconchs well illustrated by Laursen 1981, figs 18–40, pls 1, 2; Warén & Bouchet 1990, figs 85–92, 97–104). The stages of growth of the larval shell were outlined by Richter (1984). A few taxa have direct development – most notably all members of the endemic southern Australian subgenus *Sassia* (*Austrotriton*) – and several have limited enough geographic ranges to indicate that they have only short larval lives. *Cymatium parthenopeum*, one of the most widely distributed and most studied of planktotrophic molluscs, is known to have a larval life approaching a year, and to feed yet maintain a static size in the plankton (Scheltema 1966, 1971; Pechenik *et al.* 1984). It is one of several *Cymatium* species found in most warm seas – it occurs in the Mediterranean, East Atlantic, West Atlantic, South Africa, northern Indian Ocean, throughout New Zealand and southern Australia (to southern Queensland), in Hawaii, in Japan, and in the tropical eastern Pacific – but appears to be replaced ecologically in the central Pacific by *C. pileare*.

Feeding in Ranellidae has been studied by Houbrick & Fretter (1969) and Laxton (1971). Houbrick & Fretter (1969) studied the tropical *Cymatium nicobaricum*, *C. 'gemmatum'* (= *C. mundum*), *C. 'pileare'* (species uncertain; most likely to be *C. intermedium*), and *C. muricinum* in Hawaii; all species occur also in northern Australia. Laxton (1971) studied the temperate *Cabestana spengleri*, *Cymatium parthenopeum*, *Ranella australasia* and *Charonia lampas* in northern New Zealand, New South Wales and southern Queensland. *Cymatium nicobaricum* is reported to eat a great variety of gastropods (including other *Cymatium* species), *C. mundum* ate two species in the gastropod family Mitridae, and both *C. 'pileare'* and *C. muricinum* ate ostreid bivalves and species in the genus *Isognomon*. Laxton (1971) presented a table listing prey that the temperate ranellids were found to consume under natural conditions; most preferred solitary ascidians (although *Cymatium parthenopeum* also ate the bivalves *Anadara*, *Saccostrea* and *Ruditapes*), but *Charonia* species consumed only asteroids and the echinoid *Evechinus*. *Cabestana spengleri* is abundant in the intertidal zone of rocky shores in New South Wales, where it is commonly seen attached firmly to specimens of the sessile ascidian *Pyura stolonifera* ('cunjevoi'), with its proboscis deeply embedded in the ascidian.

The subfamilies are clearly monophyletic. Cymatiinae are distinguished from Ranellinae by varices situated at each 240° around the shell (a growth increment of 2/3 whorl), compared with aligned varices up the spire in Ranellinae (a growth increment of little over half a whorl, i.e. 180°–200° around the whorl). Cymatiinae are the most diverse tonnoidean group; 46 species are known from Australia. This subfamily has a mainly Tethyan fossil record (most early Cainozoic fossils occur in Europe or the South Pacific) whereas the Ranellinae evolved in the North Pacific (most early Cainozoic fossils occur in western North America, and a few in Japan and eastern Russia). The earliest ranellid genus, *Sassia*, occurs in Late Cretaceous rocks of the United States of America, Europe, and North Africa, and by Palaeocene-Eocene time had become cosmopolitan, so that long histories of several endemic species groups are preserved in Cainozoic rocks of Australia and New Zealand. It is postulated that *Sassia* gave rise to all other Ranellidae, including the earliest Ranellinae (Beu 1988).

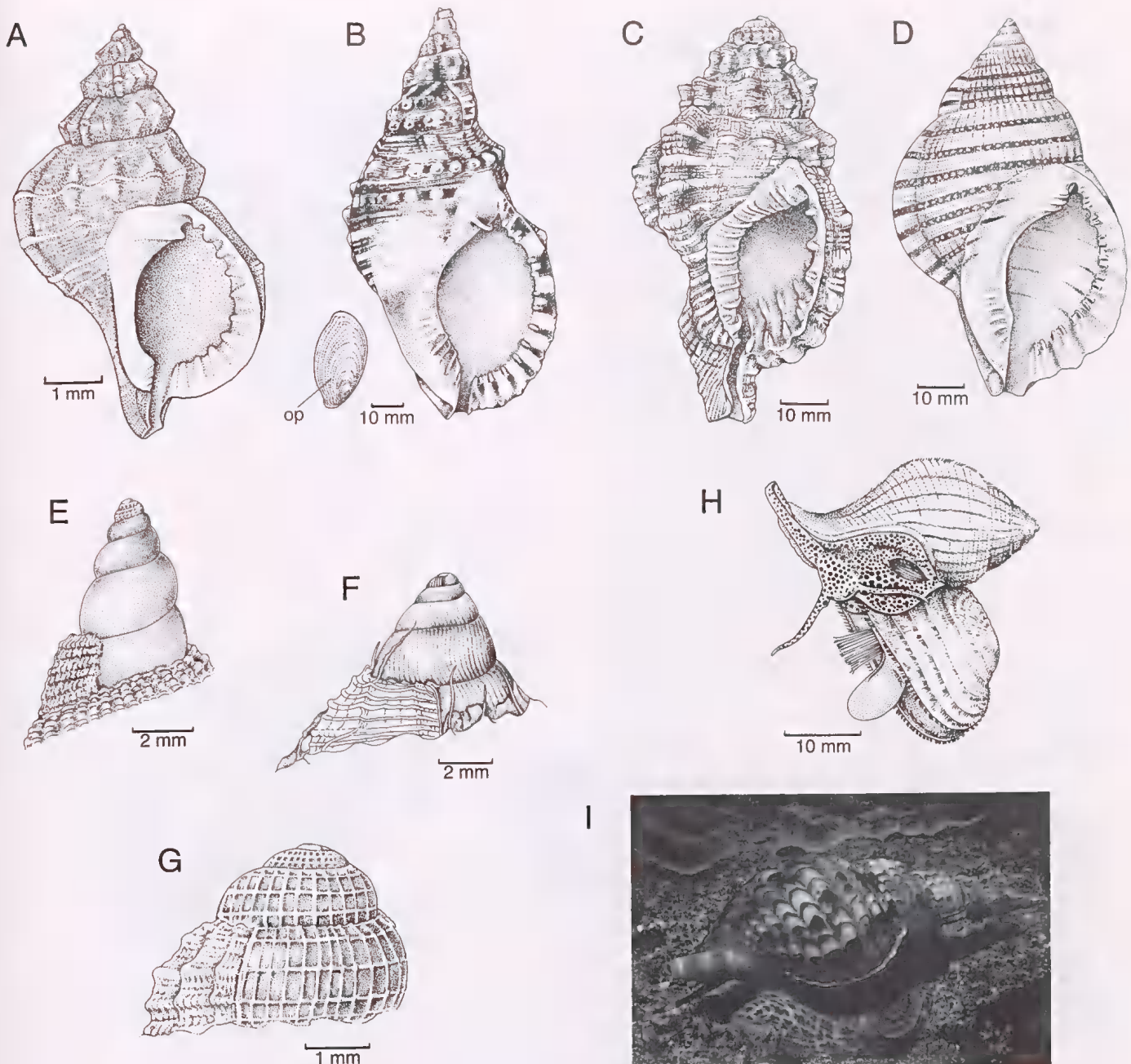


Figure 15.142 Family Ranellidae. A–D, shells, apertural view: A, *Ranella australasia*; B, *Charonia lampas*, with operculum; C, *Cymatium pyrum*; D, *Argobuccinum pustulosum*. E–G, protoconchs: E, *Cymatium intermedium*; F, *Cymatium andamanense*; G, *Sassia remensa*. H, *Linatella caudata*, feeding upon a bivalve, *Barbatia virescens*. I, *Charonia tritonis*, the largest of the Australian tritons, seen here crawling over a reef in tropical Australia. op, operculum. (E, after Beu & Kay 1988; F, after Beu 1987; G, after Beu 1978; H, after Morton, B. 1990)

The largest and best-known ranellid is the ‘Triton’s trumpet’, *Charonia tritonis* (Fig. 15.142I), which occurs nearly worldwide in the tropics. This large (to nearly 500 mm long), elongate, tall-spired species has a bright pattern of spiral rows of crescentic markings, and is unusual among epifaunal tonnoideans for its almost smooth, polished exterior, with weak sculpture of low spiral cords. It is a predator of starfish, including the coral-eating *Acanthaster planci* (see Fig. 1.31). The body is irregularly marbled with dark red blotches, and the cephalic tentacles are brightly striped with yellow and brown.

The head-foot of many other ranellids is attractively coloured. Small to large, irregular, reddish or brown blotches are seen also on *Charonia lampas*, *Sassia* and *Cabestana* species, and all Ranellinae. *Cymatium* species bear many large, conspicuous, circular spots, which are red-brown in some species, but blue-green in *C. pileare* and *C. parthenopeum*.

All ranellines have a radula with a rather simple, equidimensional, few-cusped central tooth. Two rather distinct groups are present in Australia. The first contains large, temperate species with a

circum-Southern Ocean distribution: *Argobuccinum pustulosum* in South Africa, St Paul and Amsterdam Islands, South America, Tristan da Cunha and Nightingale Islands, New Zealand and southern Australia (Fig. 15.142D); *Fusitriton magellanicus*, with the same distribution as *A. pustulosum*, although it also occurs up the east coast of Australia, and is common off New South Wales; and *Ranella australasia*, found in South Africa, Amsterdam Islands (new record), and throughout New Zealand and temperate Australia (Fig. 15.142A). The large *R. olearia* (to ca 200 mm high) occurs throughout the Mediterranean and Atlantic, in South Africa, and in New Zealand, but there are no confirmed records from Australia. A fossil species, *R. intercostalis*, occurs in Middle Miocene rocks at Muddy Creek, western Victoria.

The other group comprises the much smaller tropical species in the genera *Gyrineum* (20–40 mm high, with low but aligned varices) and *Biplex* (30–60 mm high, with the aligned varices expanded into spinose ‘wings’). The four or five *Gyrineum* species in northern Australia all occur widely in the tropical Pacific, where they are commonly dredged on the shelf, and two occur uncommonly on hard substrata in the intertidal zone.

15. PROSOBRANCHS

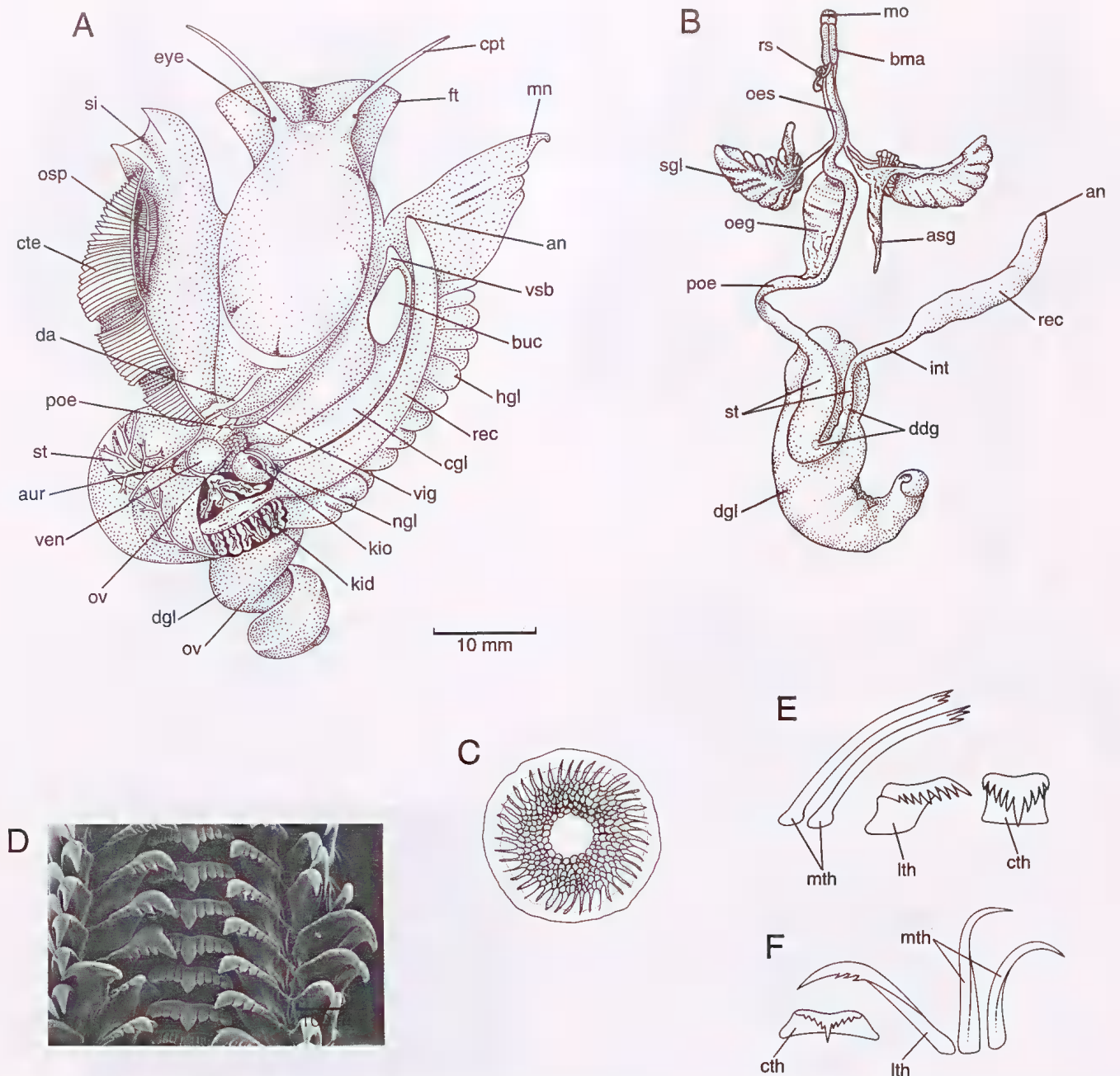


Figure 15.143 Family Ranellidae. **A**, *Ranella australasia*, dissection of female showing reproductive organs. **B**, *Ranella olearium*, alimentary tract. **C**, *Cabestana spengleri*, hemispherical egg mass viewed from above. **D–F**, portions of radulae: **D**, *Cymatium (Monoplex) aquatile*, several transverse rows of the radular ribbon; **E**, *Casmaria vibexmexicana*, half a transverse row of radular teeth; **F**, *Charonia lampas*, half a transverse row of radular teeth. an, anus; asg, accessory salivary gland; aur, auricle; bma, buccal mass; buc, bursa copulatrix; cgl, capsule gland; cpt, cephalic tentacle; cte, ctenidium; cth, central tooth; da, dorsal aorta; ddg, duct of digestive gland; dgl, digestive gland; eye, eye; ft, foot; hgl, hypobranchial gland; int, intestine; kid, kidney; kio, kidney opening; lth, lateral tooth; mn, mantle; mo, mouth; mth, marginal teeth; ngl, nephridial gland; oeg, oesophageal gland; oes, oesophagus; osp, osphradium; ov, ovary; poe, posterior oesophagus; rec, rectum; rs, radular sac; sgl, salivary gland; si, siphon; st, stomach; ven, ventricle; vig, visceral ganglion; vsb, vestibule. (A, after Laxton 1969; B, after Kilias 1973; C, after Anderson, D.T. 1959; D, from Beu & Kay 1988; E, F, after Riedel 1995)

A fossil species is common in Miocene rocks in south-eastern Australia. Three species of *Biplex* occur in northern Australia. There is no Australian fossil record of *Biplex*, but several species occur in Miocene and Pliocene rocks of Timor, central Indonesia, the Philippines and Taiwan.

Gyrineum and *Biplex* have small, turbiniform, calcareous protoconchs, with undifferentiated protoconch I and II, whereas protoconchs of the larger Southern Ocean species in other genera are markedly larger, and composed primarily of conchiolin; these latter species clearly have a planktotrophic larval stage. Planktonic veligers of *Argobuccinum pustulosum* and *Fusitriton magellanicus* have been studied in southern New Zealand waters by Pilkington (1974, 1976), and were illustrated by Warén & Bouchet (1990, figs 85, 86, 89).

A few *Cymatium* species provide the only commercially significant tonnoideans (apart from the carving of cameos from *Cypraecassis rufa*, mentioned under Cassidae). *Cymatium parthenopeum* has been

known for many years to be a predator of oysters in farm racks in Moreton Bay and nearby localities in northern New South Wales and southern Queensland (Dakin 1952). Several other species that occur commonly in northern Australia are proving to be economic pests in bivalve mariculture experiments: *C. muricinum* and *C. nicobaricum* in the Solomon Islands, and *C. martinianum* (closely related to the northern Australian *C. pileare*) in Jamaica (H. Govan & D.T.J. Littlewood personal communication).

Family Tonnidae

The Tonnidae ('tun' or 'cask shells') are a small family, represented in Australia by two species in *Eudolium*, one in *Malea*, and perhaps 10 in *Tonna*. Tonnids have large, rather thin and fragile, spectacular, subspherical shells (to ca 300 mm high in the largest *Tonna* species), with a low spire, a large enveloping last whorl, sculpture of low spiral cords only (with only fine axial riblets) and a widely open, large aperture with little or no sculpture

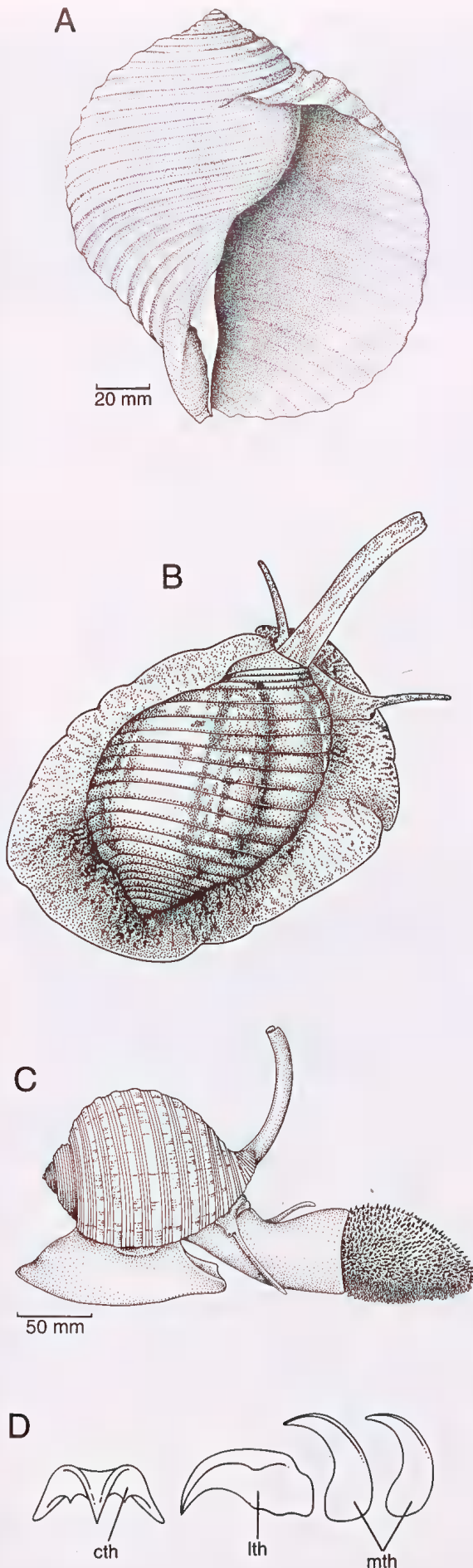


Figure 15.144 Family Tonnidae. A, *Tonna cerevisina*, shell, apertural view. B, *Tonna chinensis*, crawling with siphon extended. C, *Tonna zonata*, feeding on the sea cucumber, *Holothuria cinerascens*. D, *Tonna galea*, half a transverse row of radular teeth. cth, central tooth; lth, lateral tooth; mth, marginal teeth. (B, after Wilson & Gillett 1971; C, after Morton, B. 1991; D, after Reidel 1995)

[A, S. Weidland; B, C. Eadie; C, R. Plant; D, I. Hallam]

(outer lip narrowly thickened and flared in *Eudolium* and some *Tonna* species, widely flared and toothed in *Malea* species) and a short, widely open anterior canal (Fig. 15.144A–C). Adults lack an operculum.

The living animal and anatomy of *Tonna* were illustrated first by Quoy & Gaimard (1830–1834, pl. 41, figs 1–9). These authors (1835, pl. 41, figs 10, 11) also provided the only published illustrations of the animal of *Malea pomum*, showing it to be of a typical tonnoidean form, but with an unusually brightly banded foot; the drawings of the mantle cavity dissection show an unusually large osphradium for a tonnoidean, occupying most of the length of the mantle cavity, and apparently equal in length to the ctenidium. The dissected male has a large, blade-shaped penis with a small terminal tentacle as in *Tonna* and *Eudolium*. The anatomy of *Tonna* was later described in detail by Weber (1927) and compared with that of other tonnoideans. The animal of the male holotype of *Eudolium bairdii* was described by Verrill & Smith in Verrill (1881b, p. 300) and illustrated by Verrill (1884, pl. 29, fig. 2b); Marshall (1992) illustrated males of all three living species of *Eudolium*. The external appearance closely resembles that of *Tonna*.

In *Tonna* the foot is very large, wide and thin with anterior lateral projections, very similar to that of *Ficus* (Wilson & Gillett 1971, pl. 50, provided an excellent colour photo of the circumtropical *Tonna perdix*). The head is very wide for a tonnoidean, presumably an adaptation that accommodates the relatively short, very wide proboscis, which has a flattened, sucker-like extremity. The jaws (Warén & Bouchet 1990; Marshall 1992) are unique in having a strongly projecting anterior hook. The radulae of *Tonna* and *Eudolium* (Warén & Bouchet 1990; Marshall 1992) are closely similar, having a central tooth with a long, narrow, triangular main cusp, and projecting basal processes that interlock the column of central teeth (Fig. 15.144D; similar to those of Bursidae, but not as near the outer edges as in Bursidae). The larval shell of *Tonna* is very large (to 5 mm high) and is much like other tonnoidean planktotrophic larval shells, being composed primarily of conchiolin (Warén & Bouchet 1990, figs 73–77); that of *Eudolium* is identical (Marshall 1992). The larva, taken in plankton tows, was not associated with *Tonna* by early workers, and has been given several generic names, the best-known being *Macgillivraya*.

All *Tonna* and *Eudolium* species live in shallow to moderate depths on the continental shelf and slope, where they occupy soft substrata and are apparently buried in sediment when not feeding (Wilson & Gillett 1971). The very wide proboscis, hooked jaws and the interlocked central teeth allow ingestion of whole prey. Kropp (1982), R.N. Hughes, (1985c) and B. Morton (1991) have described the ingestion of whole, large holothurians by *Tonna perdix* and *T. zonata* (both of which occur in Australia) and it is clear that this is the normal feeding mode of *Tonna*. Grange (1974) illustrated a creeping, expanded *T. cerevisina* (a New Zealand specimen, but this is also the most common species in eastern Australia), and described the flattened proboscis tip and hooked jaws. He reported that the rectum was packed with holothurian spicules, apparently from the most common New Zealand holothurian, *Stichopus mollis*. Marshall (1992) showed that *Eudolium* species have the same wide proboscis and hooked jaws as *Tonna* and, as the gut of a specimen he examined was filled with holothurian spicules, it is clear that *Eudolium* also ingests whole holothurians.

The more robust-shelled *Malea pomum* occurs throughout the tropical Indo-West Pacific and is fairly common on beaches in northern Australia. There have been no modern illustrations or reports of living specimens and its prey and other ecological preferences are unknown.

The Tonnidae have a poor fossil record. In Australia, a single fossil *Eudolium* species, *E. biornatum*, occurs in Middle Miocene rocks at Muddy Creek, Western Victoria. In New Zealand, two Miocene *Eudolium* species are known, and there is one Late Pliocene record of *Tonna*.

Superfamily CARINARIOIDEA

Carinarioideans, otherwise known as heteropods, are the only streptoneuran gastropods, with the exception of janthinids, to have adapted successfully to a planktonic lifestyle. These molluscs have a variety of unusual morphological forms. Atlantids have a fragile, thin, compressed shell, whereas in the Carinariidae the shell is reduced, covering only the viscera, and in adult pterotracheids the shell is completely lacking. Most carinarioideans are transparent and lack pigmentation whereas others have faint pigment spots or iridophores covering the viscera and ventral surface. Adaptation to a planktonic life is evident in the streamlining of the elongate and worm-like bodies of carinariids and pterotracheids. Carinarioideans are by far the largest of the holoplanktonic molluscs: the body length in *Carinaria* species can reach 500 mm (van der Spoel 1976). The Carinarioidea comprises three families, the Atlantidae, Carinariidae and Pterotracheidae, all of which are represented in Australian waters.

Heteropods were initially considered by Lamarck (1812) to be a transitional group between cephalopods and fishes, however De Blainville (1825–1827) grouped heteropods with pteropods due to their similar planktonic behaviour. Eventually, Cuvier determined heteropods to be 'prosobranch' gastropods (Cuvier 1836 cited in Tesch 1949). The phylogenetic position of heteropods within the Caenogastropoda remains unclear. The phylogeny of heteropod taxa was discussed by Richter (1961) and by Bandel & Hemleben (1987) using evidence from radular tooth morphology and from fossils and protoconch morphology, respectively. Jamieson & Newman (1989) examined the systematic position of the Atlantidae, on the basis of sperm ultrastructure.

Heteropods swim using a relatively large fin derived from the foot to propel the animal by an undulating movement. The fin is held above the body and the eyes are projected below. But recent *in situ* and laboratory observations have shown that heteropods do not swim all the time. Carinariids have been observed rolled up in balls, suspended with the proboscis in contact with the tail (Hamner, Madin, Alldredge, Gilmer & Hamner 1975). Atlantids have also been reported to rest at the water surface or to remain suspended using mucous threads that act like a parachute (Newman 1990a).

All heteropods are active visual predators, feeding on zooplankton. The radula is taenioglossate, characteristic of neotaenioglossans (Fretter & Graham 1962; Seapy 1985). The spiked marginal teeth are used primarily for capture of prey. Richter (1968) described atlantids as 'tearers', severing prey tissue with their razor sharp lateral teeth, whereas carinariids and pterotracheids are 'swallowers', ingesting their prey whole. Atlantids are known to feed on euthecosomatous pteropods, veliger larvae and other atlantids (Richter 1968; Thiriou-Quévieux 1973; Newman 1990a). Carinariids have been found to feed primarily on salps, but also on chaetognaths (Seapy 1980). Predators of heteropods include fishes and turtles (Russell 1960; Okutani 1961; Richter 1982).

All heteropods are dioecious and exhibit sexual dimorphism. Male atlantids are distinguished by the bilobed penis on the right side of the neck, and an oval spermatophore which can be seen clearly through the transparent shell. Male pterotracheids have a small fin sucker on the anterior margin of the fin. The method of spermatophore transfer is not understood as virtually nothing is known about the reproductive behaviour of these molluscs. Gravid females deposit eggs in a floating mucous string and one pterotracheid, *Firoloida*, has been observed to carry a permanent egg string (Owre 1964). Veligers hatch with a bilobed velum which is used both for swimming and for collecting food. At metamorphosis, the velum has six lobes and is ingested (Pilkington 1970). Shell-less species cast off their larval shell at metamorphosis (Richter 1968).

Approximately 25 heteropod species occur worldwide in tropical and subtropical waters. Their distribution is generally restricted to between 40°N to 40°S and they are epipelagic, rarely being found

below 200 m (van der Spoel 1976; van der Spoel, Newman & Estep 1997). Numerically, heteropods represent a small proportion of the zooplankton and they are rarely the focus of plankton studies (Thiriou-Quévieux 1973; Seapy 1974). Virtually nothing was known, until recently, about the distribution of heteropods within Australian waters. Heteropods were recorded by Russell & Coleman (1935) for the waters of the Great Barrier Reef, Tesch (1949) for the east coast, Blackburn (1956) for Bass Strait, and Ralph (1957) for New Zealand waters.

Newman (1990a, 1990b) recently reported 20 species, all newly recorded, and in addition she extended ranges of known species (by > 1000 km). *Atlanta gaudichaudi* was found to be the most common heteropod in the waters of the Great Barrier Reef. Veligers represented over 80% of the heteropods collected in surface waters. Pterotracheids, especially *Firoloida desmaresti*, were commonly found in the Gulf of Carpentaria, whereas carinariids were exceedingly rare in all Australian waters (Newman 1990a, 1990b). The apparent rarity of these extremely large zooplankters may be due to net avoidance or preference for greater depths (Seapy 1990).

The taxonomy and systematics of the Carinarioidea is in need of review. Atlantid identifications are based on a suite of characters including sculpture of the apical whorls (best revealed by scanning electron microscopy), eye morphology, and opercular structure. Carinariids and pterotracheid species are differentiated on general morphological features such as the shape of the body, fin and visceral nucleus, and the number of gills. The fragile aragonite shells of atlantids and carinariids are often damaged after collection; they should be preserved and stored in 70% ethanol. Pterotracheid and carinariid bodies should be preserved in 3 to 5% buffered formalin. *In situ* observation and hand collection of live animals is imperative in order to understand their biology. Heteropod taxonomy has been reviewed by Thiriou-Quévieux (1973), Richter (1974), van der Spoel (1976), Bandel & Hemleben (1987), Newman (1990a, 1990b), Seapy (1990) and van der Spoel *et al.* (1997). Detailed morphological studies were undertaken by Gegenbaur (1855) and organogenesis was reviewed by Thiriou-Quévieux (1969, 1973).

Family Atlantidae

Atlantids, unlike members of the other two heteropod families, have a compressed dextrally coiled shell into which they can retract completely (Fig. 15.145A–D). The shell is distinctive in being completely transparent and planispiral with a thin keel surrounding the teleoconch or last whorl. The aperture is expanded and a thin operculum is present. The protoconch is generally covered in fine spiral sculpture, visible only under scanning electron microscopy, and used for species differentiation. Shell diameter can reach 11 mm for the largest species, *Atlanta peroni* (van der Spoel 1976).

There are approximately 15 extant atlantid species, all with similar shell shape, assigned to three genera. The main generic differences are in the composition of the shell material. *Oxygyrus* has a completely cartilaginous and flexible teleoconch (Fig. 15.145A); *Protatlanta* has a cartilaginous keel and calcareous protoconch; and *Atlanta* has a completely calcareous shell (Fig. 15.145B–D). The latter, with over 15 species, is the most common and widely distributed genus.

The well-developed head, with conspicuous eyes, eye tentacles and snout, extends from the aperture when the animal is swimming or floating (Fig. 15.145D). There is a single fin with a well-developed fin-sucker. The fin is used primarily for swimming and is held above the head so that the eyes are directed downwards. The foot, with its thin operculum, extends below the fin. The thin keel surrounding the teleoconch probably acts as a stabiliser. The eyes are large with a round clear lens and brown-black, conical retina. Both eyes can be rotated easily, scanning the water column.

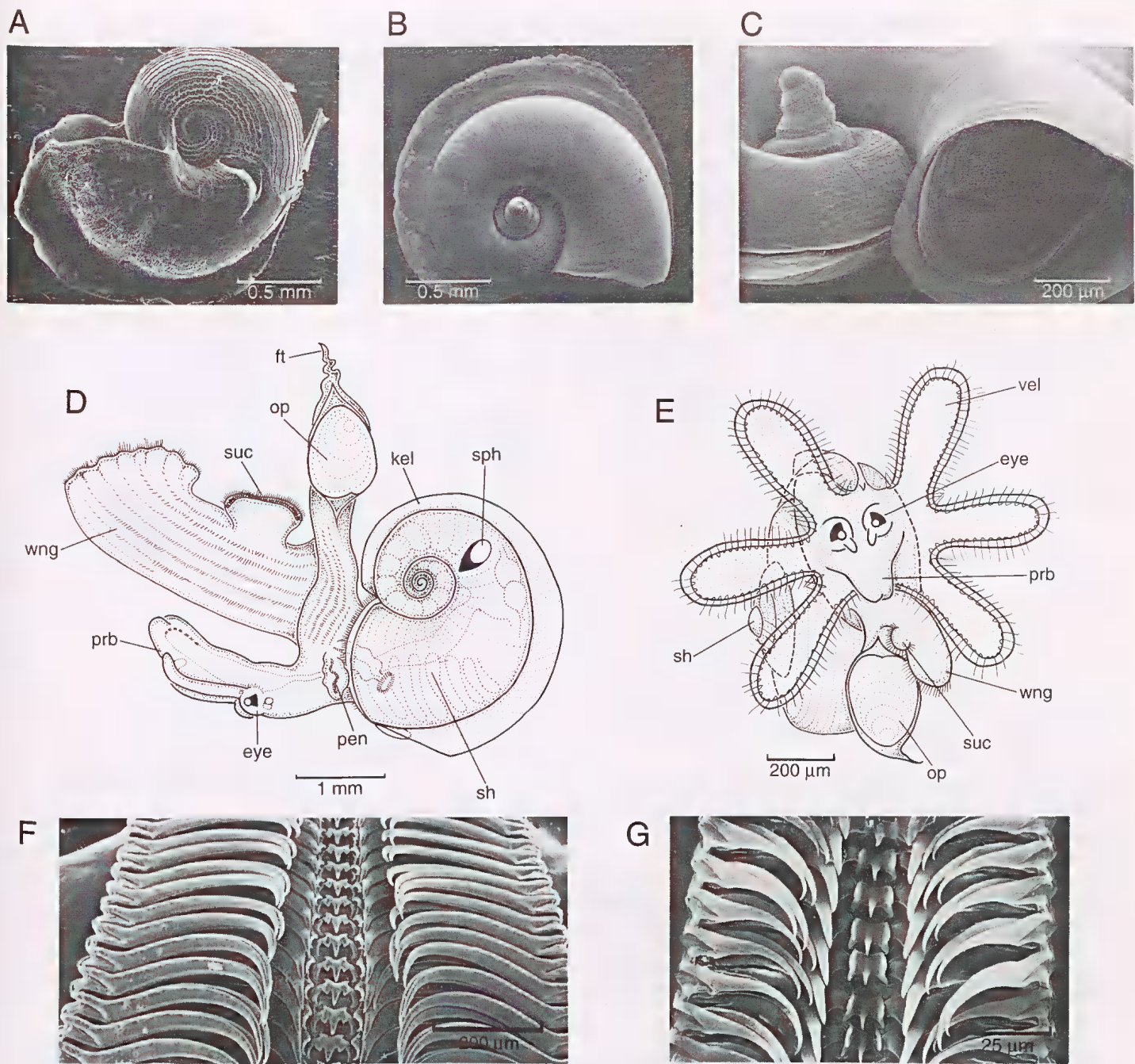


Figure 15.145 Family Atlantidae. A, *Oxygyrus keraudreni*, shell, ventral view. B, C, *Atlanta turriculata*, shell: B, dorsal view; C, apertural view. D, *Atlanta gaudichaudi*, male. E, veliger. F, G, portion of radular ribbon: F, *Oxygyrus keraudreni*; G, *Atlanta gaudichaudi*, female. eye, eye; ft, foot; kel, keel; op, operculum; pen, penis; prb, proboscis; sh, shell; sph, spermatophore; suc, sucker; vel, velum; wng, wing. (D, after Jamieson & Newman 1989; E, after Newman 1990a) [L. Newman]

Atlantids are active carnivores and voracious predators. Live atlantids have been observed feeding on euthecosomatous pteropods, veliger larvae and smaller atlantids. The fin-sucker is used to grasp the prey's shell aperture as the head reaches into the shell (see Fig. 1.51). The prey's body is eventually pulled out of its shell by the radula which is situated at the distal end of the proboscis. If the prey is too large, its tissues are severed with the razor sharp radular teeth (Thiriot-Quévieux 1973; Newman 1990a).

A single ctenidium located in the mantle cavity aids in gaseous exchange. All the internal organs are clearly visible through the transparent shell. The gonads and digestive glands are located in the apical whorls. The heart, kidney and stomach are situated anterior to the gonad.

Mature males can be distinguished by a conspicuous bilobed penis on the right side of the neck and an oval spermatophore located in the accessory gland on the right side near the kidney. The fin-sucker is thought to be used for attachment of copulating pairs although this has not actually been observed *in situ* (Lalli & Gilmer 1989). Fertilisation is thought to be internal, but the process of transfer of the spermatophores to the females is not yet understood.

Eggs are laid in a floating gelatinous mass. Newly hatched veligers have a bilobed velum which eventually develops into six lobes prior to metamorphosis (Fig. 15.145E). This velar shape is characteristic of gastropod larvae with an extended planktonic life. At metamorphosis, the velum is consumed and the fin develops (Thiriot-Quévieux 1967; Pilkington 1970; Newman 1990a).

Species identifications are based primarily on shell characteristics such as the shape and angle of the apical whorls, shell surface sculpture, the shape of the operculum and the morphology of the eyes. Many of these fine details can only be seen with the aid of scanning electron microscopy (Newman 1990a; Seapy 1990). Differences in radular tooth morphology have also been used to separate species (Fig. 15.145F, G; Richter 1986, 1987, 1989). As with the fragile pteropods, preservation problems are encountered with the decalcification of the aragonite atlantid shells. Tokioka (1955, 1961) developed a whorl formula for measurement of decalcified whorls and shape of the opercula. Van der Spoel (1972) also provided a key based on the shape of the whorls and eyes. Taxonomic reviews of atlantids were made by Thiriot-Quévieux (1973), Richter (1974, 1986, 1987, 1989), van der Spoel (1976), Newman (1990b) and Seapy (1990).

15. PROSOBRANCHS

Atlantids are circumglobal, tropical and subtropical in distribution, however, few have been reported from Australian waters. Tesch (1949) first recorded the distribution of heteropods in Indonesian and northern Australian waters. Russell & Coleman (1935) recorded *A. peroni* from northern Great Barrier Reef waters. Newman (1990a, 1990b) found that atlantids are common within the Great Barrier Reef and the Coral Sea, adding eight new species records and extending the ranges of many species. The most common species for both east and west coasts of Australia is *A. gaudichaudi* (Fig. 15.145D) which occurs from the North West Shelf (Western Australia) across the top of Australia to the south-eastern coast of New South Wales. Richter (1974) documented atlantids from the Indian Ocean.

Atlantids have a rather patchy fossil record extending back to the Eocene, and possibly to the Late Cretaceous. One species, *Atlanta fossilis* is known from Cape Otway, Victoria (P. Maxwell personal communication). Some fossil species lack a distinctive peripheral keel, although the last whorl is usually somewhat compressed.

Family Carinariidae

The carinariid heteropods are fascinating and bizarre looking planktonic gastropods that are rarely found within Australian waters. Members of this family are cylindrical and have a distinctive head, trunk and tail. The visceral mass is situated towards the posterior end and is covered by a small fragile shell into which the animal can never retract (Fig. 15.146A–C). Carinariids are rarely found with their delicate shell intact (as in Fig. 15.146D), and consequently the shells are highly prized by collectors. Animals vary in length from 20 mm to an astounding 0.5 m for the largest heteropod, *Carinaria cristata* (van der Spoel 1976).

Systematically, carinariids are placed between the shelled atlantids and the shell-less streamlined pterotracheid heteropods on the basis of their reduced shell (van der Spoel 1976).

All the internal organs are located posteriorly within the stalked visceral mass. The filamentous external gills are attached anteriorly to the mantle, and the osphradium is at the base of the gills. The heart and kidney are situated anteriorly. The digestive gland is cylindrical, the anus is situated dorsal to the digestive gland and the renal opening is posterior to this gland (van der Spoel 1976).

These animals have the largest eyes of all heteropods. The large swimming fin, with its fin-sucker, is positioned above the body such that the eyes project below. Eye tentacles occur in both sexes but can be unequal in length (Pafort-van Iersel 1983). Swimming is effected by undulation of the body and flapping of the large fin. The gelatinous nature of carinariids aids in buoyancy control in a similar manner to that in jellyfish (Aravindakshan 1973), and their transparency is their principal defence against predation (Hamner *et al.* 1975; Seapy & Young 1986).

Attack behaviour, involving rapid swimming and seizure of prey, has been observed *in situ* by Hamner *et al.* (1975). Once captured, the prey is pulled into the oesophagus by the radula, or tissue is severed by the spiked and razor-sharp lateral teeth (Fig. 15.146E). The oesophagus runs from the muscular buccal mass through the trunk to the visceral nucleus. Carinariids prey mainly on salps, but chaetognaths, pelagic nudibranchs, euphausiids, copepods and pterotracheids are also eaten (Hamner *et al.* 1975; Seapy 1980). Turtles and tuna have been observed to eat carinariids (Okutani 1961; Hamner *et al.* 1975). Cannibalism may occur if the prey is less than half the size of the predator (Seapy 1980).

Carinariids are dioecious and males are distinguished by a trilobed penis on the right side near the visceral nucleus. Spermatophore transfer is not understood (van der Spoel 1976). According to Tesch (1949), fertilisation is internal and the eggs are deposited in strings that are carried by the female.

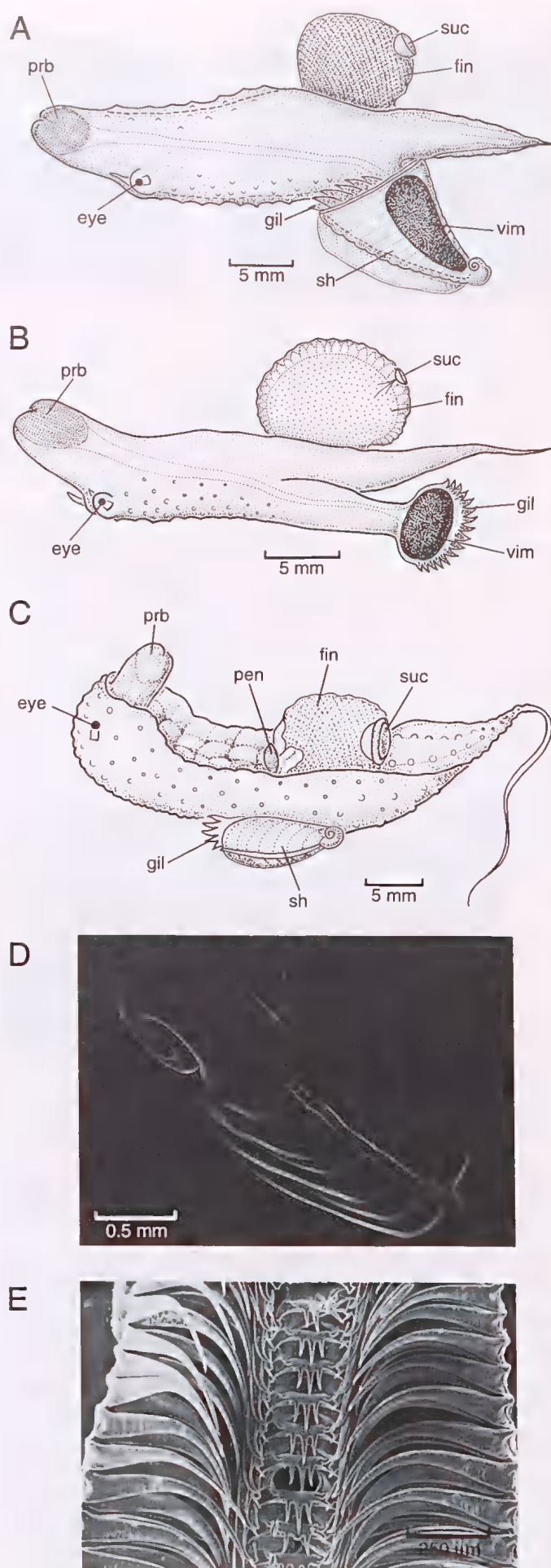


Figure 15.146 Family Carinariidae. A–C, animals: A, *Carinaria cithara*; B, *Cardiapoda placenta*; C, *Pterosoma planum*. D, *Pterosoma planum*, shell. E, *Carinaria galea*, portion of radular ribbon. eye, eye; fin, fin; gill, gill; pen, penis; prb, proboscis; sh, shell; suc, sucker; vim, visceral mass.

[L. Newman]

Heteropods are generally thought to be surface-dwelling solitary animals, rarely being found below 100 m. Dales (1953) found that carinariids are characteristic of plankton communities consisting mainly of salps, jellyfishes and chaetognaths and are only rarely found in plankton dominated by copepods, euphausiids or other Crustacea.

All three genera in the family occur in Australian waters, represented by six species. Species of *Carinaria* have been recorded from the North West Shelf, Indonesia and the Tasman Sea. Species of *Cardiapoda* and *Pterosoma* occur from tropical Indonesian waters through to the Tasman Sea (van der Spoel 1976; Newman 1990b; van der Spoel *et al.* 1997). Records are scarce and these heteropods are uncommon in Australian waters.

Species identifications are based on the morphology of the body, eyes, gills and fin. The shell, when found attached, is the most useful taxonomic feature. *Carinaria* species have a cap-shaped shell, its length approximately one-fifth of the body length (Fig. 15.146A); the tail region is well developed and extends into a crest in some species (Fig. 15.146A). In *Cardiapoda* species, the shell is small, round and cartilaginous and the aperture is greatly expanded; the visceral mass is characteristically rounded with numerous gills (Fig. 15.146B). In *Pterosoma* species, the shell and visceral mass are dorso-ventrally flattened and the mantle is flared into a gelatinous shield (Fig. 15.146C). Comprehensive reviews of carinariids are given by van der Spoel (1976) and Pafort-van Iersel (1983), and feeding studies by Seapy (1980).

Fossil carinariid shells are known from the early Jurassic of southern Germany (Bandel & Hemleben 1987).

Family Pterotracheidae

Pterotracheid heteropods are the most streamlined of the pelagic gastropods and it is difficult to imagine that these extraordinary animals are actually molluscs. Unlike other heteropods, adult pterotracheids do not have a shell. The body is slender, elongate, and highly transparent and the animal may, on first appearance, resemble a chaetognath (Fig. 15.147A–C). The eyes are not as conspicuous as in the other two families, but their structure is similar, with a darkly pigmented retina and clear lens. The proboscis is long, narrow and highly mobile. The swimming fin is round and large, with a small fin-sucker found only in males. The visceral nucleus is located posteriorly and is not stalked as in carinariids. A tail is located posterior to this visceral nucleus. There are no eye tentacles in the genus *Pterotrachea*; although tentacles are found in male *Firoloida*. The family is represented by the two genera *Pterotrachea* (Fig. 15.147A, B) and *Firoloida* (Fig. 15.147C), the latter being commonly found in Australian waters. Animals can reach up to 200 mm in total body length.

Pterotracheids are highly adapted for floating. Hamner *et al.* (1975) observed *Firoloida desmaresti* curled up in balls, the radula in contact with the shortened tail when they are not actively chasing prey. When the animal is swimming, the fin flaps above the body and the eyes project downward. In these surface-dwelling animals the arrangement of the eyes facilitates location of prey.

Pterotracheids are active predators and are strictly carnivorous. Their prey consists of zooplankters such as smaller atlantids, pteropods and larval and juvenile fish. Studies on *Pterotrachea coronata* showed the principal food items to be siphonophores, copepods, chaetognaths and ostracods (Hamner *et al.* 1975). These pterotracheids migrate vertically to follow their prey (Aravindakshan 1973). According to van der Spoel (1972), pterotracheids are highly adapted to detect their prey visually and are commonly found in the upper photic layers. Seapy & Young (1986) found that concealment is also enhanced by the long and slender visceral nucleus which is covered by a reflective layer similar to that found in pelagic squid.

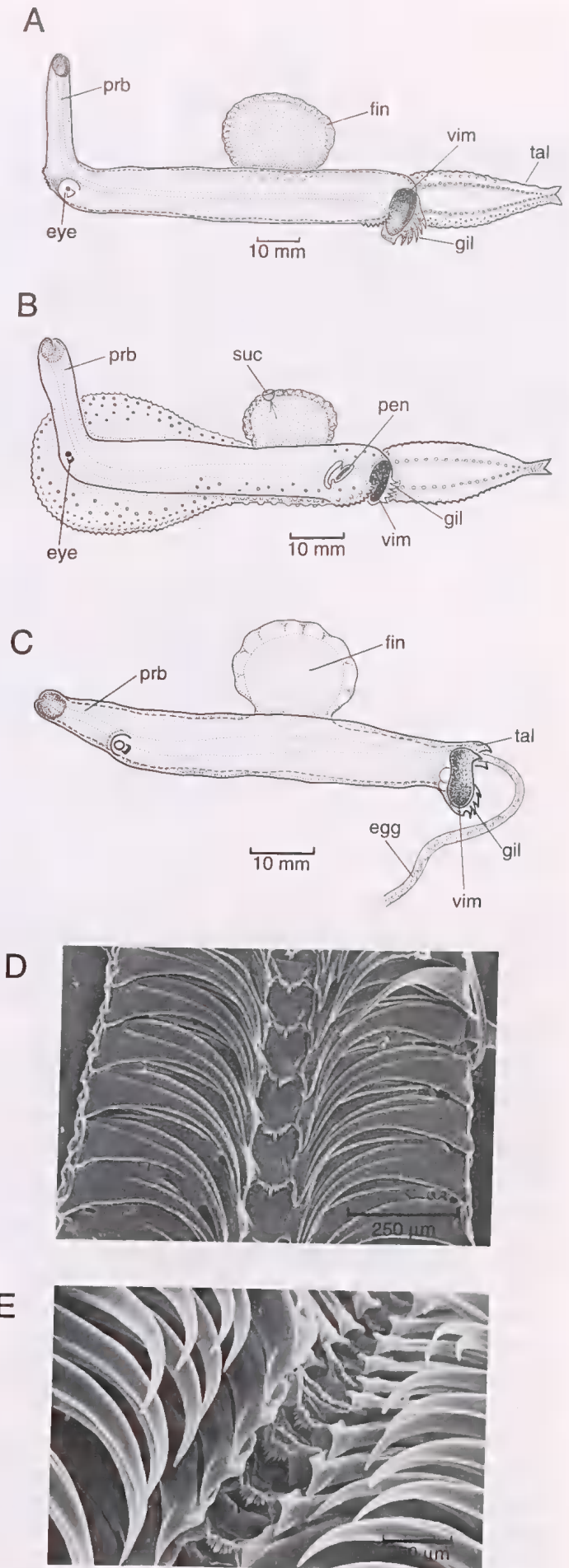


Figure 15.147 Family Pterotracheidae. A–C, animals: A, *Pterotrachea hippocampus*, female; B, *Pterotrachea scutata*, male; C, *Firoloida desmaresti*, female with attached egg-string. D, E, portions of radular ribbon: D, *Pterotrachea coronata*, male; E, *Firoloida desmaresti*, female. egg, egg string; eye, eye; fin, fin; gill, gill; pen, penis; prb, proboscis; suc, sucker; tal, tail; vim, visceral mass. [L. Newman]

15. PROSOBRANCHS

The radula can be everted by buccal muscles to expose the spiked lateral teeth (Fig. 15.147D, E) which entangle the prey and draw it into the buccal cavity (Tesch 1949). The arrangement of the internal organs is similar to that of carinariids except that the visceral mass is cylindrical and not covered by a shell. The gills are located posteriorly and are attached dorsally to the visceral mass. The number and arrangement of these external gills is species specific: *Pterotrachea hippocampus* has many gills, *P. coronata* usually eight and *P. scutata* has only a few.

The penis is located on the right side near the visceral mass. Fertilisation is thought to be internal. The female opening is dorsal to the anus (Tesch 1949). Female *Firoloidea* carry a permanent egg string which is attached to the shortened tail (Fig. 15.147C; Owre 1964). The embryos develop within the egg string and those towards the distal end hatch free as veligers. According to Pilkington (1970) larvae are similar in all heteropods and have a two lobed velum that develops into six lobes at metamorphosis. The larval shell is assumed to be cast off at metamorphosis.

Pterotracheids can be so numerous at times that they form dense aggregations causing sonic scattering layers in the upper 20 m in Bass Strait (Blackburn 1956). Lester & Newman (1986) reported the first digenean trematode rediae and cercariae to be found in heteropods, in *F. desmaresti* from the Gulf of Carpentaria, suggesting that heteropods may be an abundant primary host of parasites found in pelagic fish.

Tesch (1906, 1949) first recorded heteropods from Australian waters. Newman (1990b) found that all pterotracheid species are represented within Australian waters; she gave nine new records and extended ranges. The most common and widespread species is *F. desmaresti* which has been found off northern Western Australia and from the Gulf of Carpentaria through to the Tasman Sea. Aravindakshan (1977) reported *P. coronata* and *P. hippocampus* (Fig. 15.147A) to be common in waters off Western Australia and *P. scutata* (Fig. 15.147B) has been recorded from eastern Australian waters (van der Spoel 1976; Newman 1990b).

Species identifications are based on morphological characteristics such as size and shape of the visceral mass, eyes, length of tail and proboscis. Taxonomic reviews of this family are provided by van der Spoel (1976), Pafort-van Iersel (1983) and Seapy (1985).

Infraorder PTENOGLOSSA

The Ptenoglossa (= Ctenoglossa) is almost certainly a paraphyletic or polyphyletic taxon. It includes Triphoroidea, Janthinoidea and Eulimoidea. Most members have an acrembolic proboscis and a characteristic 'ptenoglossan' radula, although the radula in Cerithiopsidae, probably the most primitive family in the group, is very variable and many are taenioglossate (Marshall 1978; Bouchet & Warén 1993). Members of the Triphoroidea and Janthinoidea have distinctive parasperm (Healy 1988a, 1990b); whereas the Eulimoidea have no parasperm (Healy 1988a).

Little is known about the anatomy of ptenoglossans and virtually no developmental data are available, other than a few descriptions of larvae. Little information is available even for janthinoideans (Taki 1956, 1957; Fretter & Graham 1962; Graham 1954a, 1965a). The anatomy of the Eulimoidea is better known (see Ponder & Gooding 1978 and Warén 1983a for review and references and Warén 1983b). However, eulimoideans have a very doubtful relationship with other ptenoglossans (Healy 1988a; Ponder & Warén 1988; Bandel 1993a) and it is unlikely that Triphoroidea and Janthinoidea are closely related. Whereas no triphoroidean is known to have a penis, this structure is found in eulimoideans and a few primitive epitoniids.

Ptenoglossans are, in some features, similar to cerithioideans and various anatomical characters show convergence with those of tonnoideans and neogastropods, notably the formation of a proboscis (and associated foregut changes) and simplification of the stomach. E.B. Andrews (1991) has argued that Ptenoglossa and Neogastropoda share some synapomorphies, namely purple

hypobranchial secretion and accessory salivary glands, but these putative homologies have yet to be examined critically. Robertson (1985b) argued that janthinoideans are allied to architectonicoideans based on an assumed homology of the pallial purple gland with the pigmented mantle organ, and the chalaza-like structures in the egg mass; none of these structures is homologous with the apparently similar structures in heterobranchs (Haszprunar 1988a). Bandel (1993a) discussed the fossil history of the group, which extends from the Carboniferous.

Superfamily TRIPHOROIDEA

The shells of members of this superfamily are small (usually less than 10 mm, but can be up to 40 mm or more), typically very high spired, with numerous whorls, and mostly spiral or clathrate sculpture. The shells can be dextral or sinistral, and have a multi-whorled protoconch (if not direct-developers) and an anterior canal. They are marine, mostly shallow-water animals, being particularly diverse in tropical and temperate habitats. Some species live in deep water (up to 1000 m; Marshall 1983c). Both the Cerithiopsidae and Triphoridae, the most diverse families, are sponge feeders with an acrembolic proboscis, have open, partially open or closed pallial gonoducts, and are aphyallic (Fretter 1951b; Kosuge 1964, 1966a). Sperm of the families Triphoridae and Cerithiopsidae are similar (Healy 1988a), both having spermatozoeum, and in this respect, and a number of others (see below), differing from cerithioideans.

Until recently, triphoroideans were included in the superfamily Cerithioidea due to similarities in shell features and sharing of certain plesiomorphic anatomical features, including open pallial ducts (although triphorids have closed genital ducts – see under Triphoridae) and the absence of a penis (Fretter 1951b). However, Kosuge (1964, 1966a), citing the acrembolic proboscis, oesophageal pouch, radular characteristics, and spiral operculum, established the new superfamily Triphoroidea for the Triphoridae. Kosuge (1964) initially placed the Triphoroidea in the Mesogastropoda, but later transferred the superfamily to a new higher grouping he called Heterogastropoda, which was placed between the Mesogastropoda and the Neogastropoda (Kosuge 1966a). Marshall (1977a, 1977b) subsequently referred the Triforidae to the Triphoroidea, which he also included in the Heterogastropoda; by then heterogastropods were thought to be primitive opisthobranchs. The name Heterogastropoda is no longer used and families originally assigned to it have been distributed among other groups of gastropods. Marshall (1980) subsequently placed the Triforidae in the Cerithiopsidae. Here Triforidae are included in Cerithiopsidae.

Marshall (1983c) noted that most triphorids could be easily distinguished from cerithiopsids by their sinistral shell and the presence of a posterior canal. However, some triphorids are dextral, lack the posterior canal and resemble cerithiopsids in shape. They can usually be distinguished by the presence of a columellar plait, but the correct placement of some species will remain uncertain until radulae are studied. Cerithiopsids have a taenioglossate radula (seven teeth per row), but the triphorid radula is unique with five to 63 teeth per row (Marshall 1983c). Whereas Gründel (1980) and Marshall (1980, 1983c) distinguished both Triphoroidea and Cerithiopsidae, Ponder & Warén (1988) recognised only a single superfamily, Triphoroidea, including four families: Cerithiopsidae, Triphoridae, Triforidae and (tentatively) Sherborniidae (following Marshall 1980). The latter family is now subsumed in the Pickworthiidae which is included tentatively in the Littorinoidea. The relationships between triphoroideans are poorly understood and the family-level classification requires revision (Bouchet & Warén 1993).

All triphoroideans are primarily sponge feeders (Fretter 1951b; Marshall 1978, 1983c) but juveniles have been observed feeding on diatoms and other surface films (Lebour 1933a; Fretter 1951b). Fretter (1951b) pointed out that evolution of a long, narrow proboscis has given cerithiopsids and triphorids access, through the osculum, to the internal part of a sponge. However, Marshall

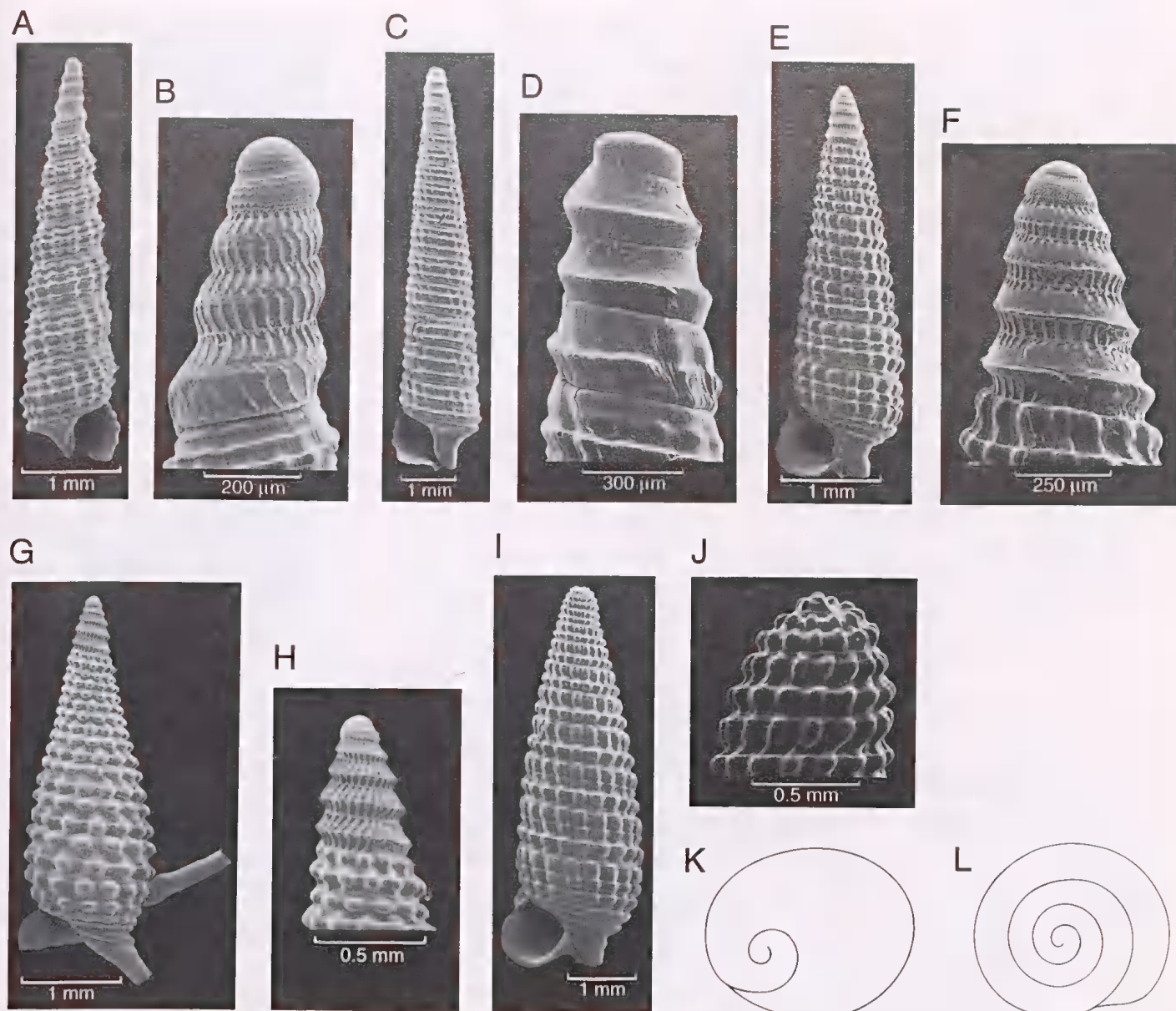


Figure 15.148 Family Triphoridae. A–J, shells and protoconchs: A, B, *Metaxia fuscoapicata*; C, D, *Inella spina*; E, F, *Hedleytriphora innotabilis*; G, H, *Mastoniaeforis* cf. *chaperi*; I, J, *Isotriphora amethystina*. K, L, opercula: K, *Aclophoropsis univitta*; L, *Isotriphora amethystina*. (K, L, after Marshall 1983c) [A–J, B. Marshall; K, L, I. Hallam]

(1983c) noted that one triphorid, *Bouchettriphora pallida*, from New Zealand, excavates large holes in a soft-textured sponge. Proboscis elongation was achieved by lengthening of the mid-oesophagus, accompanied by the spreading of the oesophageal glands along its length in at least some cerithiopsids (Fretter 1951b). In the triphorid examined by Fretter (1951b), the mid-oesophagus is narrow, the oesophageal gland having been reduced in a manner somewhat analogous to that seen in neogastropods. The stomach is a simple ciliated sac that receives two ducts from the digestive gland.

Family Triphoridae

Triphorids are the only large group of marine gastropods that are predominantly sinistral and in this feature, are unlike members of the Cerithiopsidae. Shells (Fig. 15.148A, C, E, G, I) are small, usually less than 10 mm long, but can be up to 40 mm or more in length, with a high spire, numerous whorls, a short to long anterior canal and a posterior apertural notch or canal. The apertures of a few species have a tubular, dorsally directed posterior canal. There is considerable variation in the teleoconch sculpture of triphorids, with some species being beaded, others spinose, still others reticulate, and some having prominent spiral cords with little axial sculpture. In addition, a few triphorids have a distinct microsculpture of fine granules.

Some triphorids have dextrally coiled shells, among them the genera *Metaxia* (Fig. 15.148A) and *Seilarex* in Australia (Marshall 1977b, 1983c).

The importance of the protoconch shape and sculpture in triphorid systematics was emphasised by Marshall (1983c). Some species have multispiral protoconchs, indicating planktotrophic development (Fig. 15.148B, D, F, H, J), others are paucispiral indicating lecithotrophic or direct development. Protoconch form may vary at generic level, but is constant for species. The present classification of triphorids is largely based on a combination of teleoconch, protoconch and radular characters.

Fretter (1951b) and Kosuge (1977) have provided general accounts of the anatomy of members of the family, Kosuge examining 16 species in seven genera. The head-foot is rather simple (Fig. 15.149A–C), the head lacks a snout and has slender cephalic tentacles with the eyes at their outer bases. The narrow foot (Fig. 15.149B) has a well-developed posterior pedal gland and slit, and an anterior propodium beneath which the large anterior pedal gland opens. There are no pedal or pallial tentacles.

The operculum (Fig. 15.148K, L) is thin, horny and circular to elliptical with a central to eccentric nucleus and, in a few taxa, bears a peg on the inner surface.

15. PROSOBRANCHS

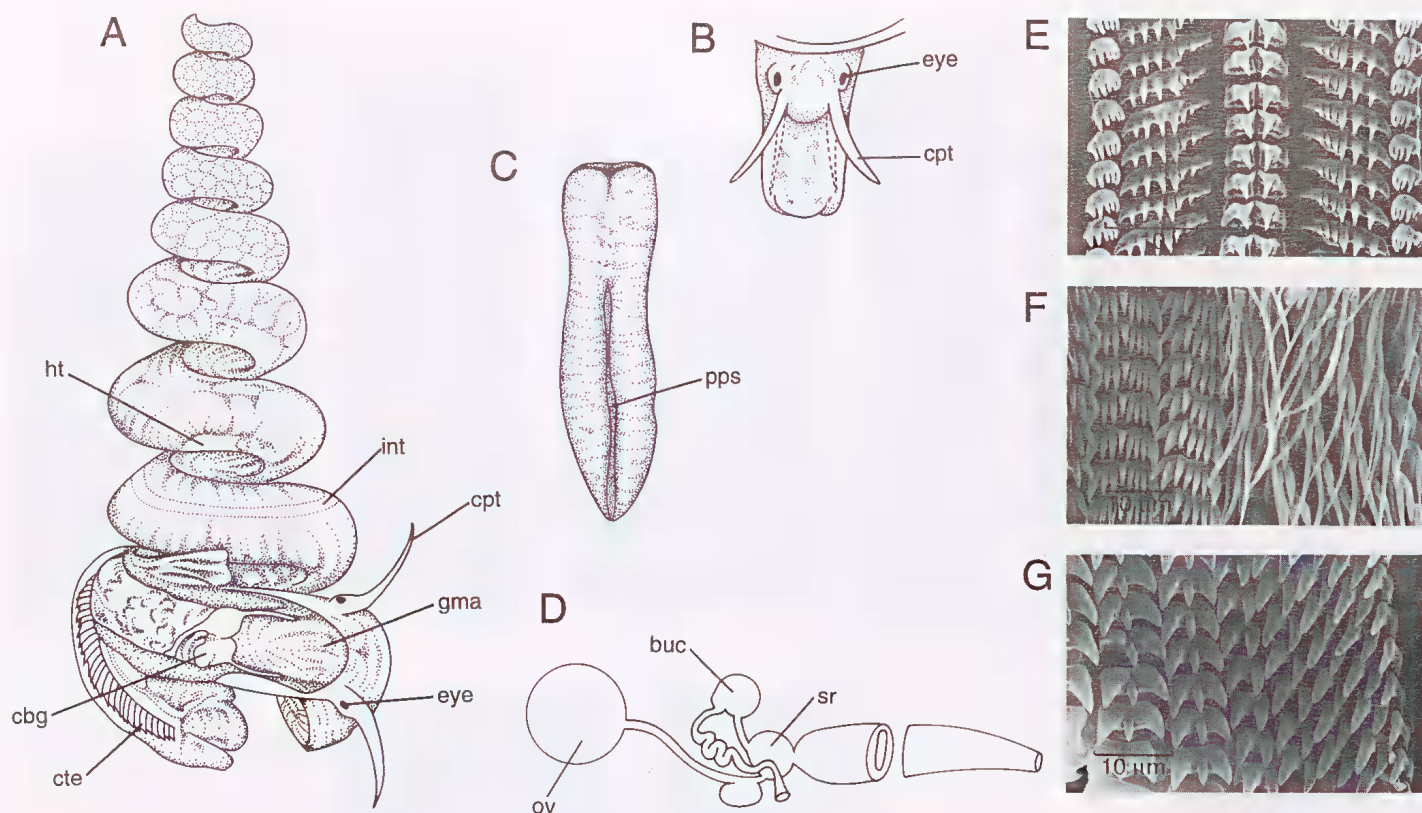


Figure 15.149 Family Triphoridae. A–C, *Mastonia limosa*, internal and external features: A, body with shell removed, mantle and body wall cut open dorsally in body whorl; B, head, anterior part; C, foot, ventral view. D, *Triphora contrerasi*, reconstruction of the female genital duct. E–G, portions of radular ribbons: E, *Sagenotriphora ampulla*; F, *Bouchettriphora pallida*; G, *Aclophora hedleyi*. alb, albumen gland; buc, bursa copulatrix; cbg, cerebral ganglion; cpt, cephalic tentacle; eye, eye; gma, gelatinous mass; ht, heart; int, intestine; ov, ovary; pps, posterior pedal slit; sr, seminal receptacle. [A–D, I. Hallam; E–G, B. Marshall]

Triphorids are sponge feeders with an extensible acrembolic proboscis. The oesophagus is modified by being lengthened, with the oesophageal glands of the mid-oesophagus reduced and removed from the food channel, and the salivary glands opening, more posteriorly than in other gastropods, into the glandular region of the oesophagus (Fretter 1951b).

There are large paired jaws and a rather short radular ribbon. The radula (Fig. 15.149E–G) shows great diversity within the family and is so unusual that it has been distinguished by the term rhinoglossate. There is a single central tooth, one pair of laterals, and one or more pairs of minute marginal teeth, giving a range of from five to 63 teeth per row (Marshall 1983c). The teeth typically bear one or more long, sharp spines.

The reproductive systems have been described by Johansson (1953), Kosuge (1966a) and Houston (1985). The female system (Fig. 15.149D) is reported to have an open pallial glandular duct in some species (Fretter 1951b; Houston 1985), however, Johansson (1953) and Kosuge (1977) showed it to be a closed tube. There is a large posterior bursa copulatrix and seminal receptacle. A sperm duct from the posterior end of the mantle cavity enters the bursa copulatrix which itself opens to the oviduct by way of the bursal duct. The location of the seminal receptacle varies, opening either to the oviduct just behind the bursal duct or at the anterior end of the bursal duct. The male pallial duct is also a simple, closed tube (Kosuge 1977; Houston 1985).

The nerve ring lies behind the head and exhibits some concentration of the ganglia (Kosuge 1977). The cerebral ganglia are larger than the pedal ganglia and both the supra- and suboesophageal ganglia are separated from the pleural ganglia by moderately long connectives.

Triphorids are common under rocks and dead coral slabs in shallow water, with some species living as deep as 1000 m. The family is diverse, possibly comprising as many as 1000 species. An indication of the diversity of the family is that a single sand sample collected on the Great Barrier Reef contained 80 triphorid species (Marshall 1983c).

The larval development of a European species was described by Lebour (1933a) and Thorson (1946) and the larvae (in the species studied) are planktotrophic. The spawn of only one European species has been described and consists of gelatinous capsules laid in one layer (Pelseneer 1926). Protoconch morphology indicates that some taxa have direct development (Marshall 1983c).

Laseron (1958) greatly increased the number of generic names available for triphorids, and the classification of the family was further developed by Kosuge (1966a), Gründel (1975) and Marshall (1983c).

There were several taxonomic studies of triphorids in Australia early in this century. The most recent papers are those of Laseron (1954b, 1958) and Marshall (1983c). In the earlier paper, Laseron (1954b) recorded 28 species in five genera from New South Wales, and in the later paper (Laseron 1958) he examined species from the entire coastline of northern Australia. One hundred and one species in 17 genera were recognised. Of these, 91 species and 11 genera were described as new. Laseron's (1958) paper also covered the Australian territory of Christmas Island (Indian Ocean), recording a fauna of 14 species in 10 genera. The most substantial paper on Australian triphorids is the work of Marshall (1983c) on the southern Australian species. He recognised three subfamilies, Triphorinae which is sinistral, and the dextral Adelacerithiinae (see Marshall 1984) and Metaxiinae. Sixty-eight species belonging to 27 genera were listed for southern Australia, of which 18 species and eight genera were described as new. Protoconch structure is crucial to the proper classification of species in the family, but the protoconch is often worn in adult specimens.

One of the interesting features of the zoogeography of southern Australian triphorids was the finding by Marshall (1983c) of a number of pairs of species, with one species of each pair living on each side of Bass Strait. The taxonomic difficulties in this group are well illustrated by what was thought to be a single species in Europe being split into several (Bouchet & Guillemot 1978; Bouchet 1985).

An overall revision of Australian triphorids has never been undertaken; there are probably several hundred taxa. As with most groups, there are separate tropical and temperate species; Marshall (1983c) recorded a single species as being circumcontinental. Generic diversity in Australian triphorids is also high, with Laseron (1958) recognising 17 genera in the north and Marshall (1983c) 27 in the south; only 10 genera were found to occur in both the northern and southern studies. Based on Laseron's study (1958), the most diverse tropical genera are *Mesophora* (17 species), *Coriophora* (16 species), *Nanaphora* (10 species) and *Notosinister* (nine species). According to Marshall (1983c), the most diverse south-eastern genera are *Inella* (six species), *Isotriphora* (six species) and *Hedleytriphora* (five species).

Marshall (1983c) considered that only a small fraction of triphorid species and genera have been described. Many fossil species have been described, however fossil taxa are very poorly known in Australia (see Darragh 1970 for list of named taxa), although well represented in Tertiary deposits there and elsewhere (see Gougerot & Le Renard 1980).

Family Cerithiopsidae

Members of the Cerithiopsidae have shells which resemble those of some cerithoideans, particularly small cerithiids such as species of *Bittium*. They are small – usually less than 10 mm, typically no larger than about 17 mm (Fig. 15.150C, F), but a few taxa are considerably larger, such as *Ataxocerithium eximium* which attains a shell length of up to 46 mm (Fig. 15.150A). The shells are high, narrow and cylindrical. Sculpture is variable, but most shells have a reticulate pattern with spiral and axial costae, the intersections beaded (Fig. 15.150B, E). Protoconchs tend to be exquisitely ornamented, but some are smooth; the variation in protoconch shape and sculpture is an important taxonomic character (Fig. 15.150D; Marshall 1978). The outer lip of the shell is not expanded and the shells have no varices (Fig. 15.150E). The operculum is thin, horny and circular with a central nucleus or ovate to triangular with a terminal nucleus (Fig. 15.150G, H).

The morphology of members of this group is very poorly known. Fretter (1951b) provides a detailed account of a European species. The head-foot (Fig. 15.150I) is similar to that of triphorids (Fig. 15.149A–C), and as in Triphoridae the foot has a posterior pedal gland and cleft.

Cerithiopsids, like triphorids, are sponge feeders (for a summary of feeding records see Marshall 1978), many having an extensible acrembolic proboscis (although it is very short in some) (Fig. 15.150J). The large salivary glands have different sizes and histologies, the left being large and complex, the right small and simple. The salivary ducts open to the buccal cavity. The oesophagus is modified by being lengthened, with a restricted diameter, and the oesophageal gland is reduced to a single strip. The radula is taenioglossate (Fig. 15.150L, M; Fretter 1951b; Marshall 1978; Houbriek 1987d).

Fretter (1951b), Johansson (1953) and Houston (1985) described the genital systems of several cerithiopsid species. They have open or partially open pallial genital ducts; a sperm groove runs along the free edge of the pallial oviduct and opens to the posteriorly located bursa copulatrix (Fig. 15.150K). There is also a posterior seminal receptacle that opens to the bursal duct, not to the oviduct as is usually the case. The male pallial duct is partially open to open.

The Australian members of this family, and indeed those in most parts of the world, are very poorly known and our current understanding of the Australian taxa is based almost entirely on shell characters. Living animals are usually found on the sponges on which they feed. A number of general references and faunal inventories contain lists of cerithiopsids. The most recent revisions of Australian species were regional, published in the 1950s. Cotton (1951) recognised 26 species from the temperate Flindersian zoogeographical province. A month after Cotton's paper was published, Laseron (1951a) independently published an

analysis of the species occurring in the Peronian region, which he largely equated to New South Wales, and recognised 42 species in seven genera, with the greatest number of species assigned to *Cerithiopsis*. Several years later, Laseron (1956b) revised the cerithiopsids of the tropical Solanderian, and to a lesser extent the Dampierian, provinces. Of the 46 species in 10 genera that he recognised, 42 species and six genera were described as new, involving a major re-assessment of the conservative treatment of genera in the earlier paper. *Joculator* with 10 species, appeared to be the most speciose genus. To date there have been no revisions of the species from other parts of Australia, although Wilson (1993) has illustrated several taxa from a range of genera. Laseron (1956b) pointed out that the species recognised in each of the three regional papers were largely distinct from each other. He speculated that when revisions become available for all Australian waters the total number of cerithiopsid species will be well into the hundreds. In contrast to the lack of a complete revision of Australian cerithiopsids, Marshall (1978) has revised all the Recent New Zealand species, recognising 37 species, in three subfamilies, Cerithiopsinae, Aliptinae, and Eumetulinae. He somewhat tentatively recognised Cerithiellidae as a distinct family and suggested that *Ataxocerithium* might be included on the basis of radular characters. *Cerithiella* and related genera are here treated as belonging to the Cerithiellinae, another subfamily of Cerithiopsidae. Bouchet & Warén (1993) noted that 'there are many problems in the present classification of cerithiellids, cerithiopsids, triforids, etc.' In the eastern Atlantic, Cerithiopsidae *sensu stricto* are not often found deeper than 200 m whereas *Cerithiella*, *Eumetula* and similar genera are typical of deeper water (Bouchet & Warén 1993) and this also appears to be so in the Australasian area.

The genus *Triforis* is rather poorly known, differing from many other cerithiopsids in having a well-developed posterior siphonal notch or tube. *Triforis* species were thought simply to be dextrally coiled triphorids, however, Marshall (1980) showed that one New Zealand *Triforis* species has a taenioglossate radula and argued for separate family status. He also pointed out the similarity of the larval shells of *Triforis* and *Ataxocerithium* and suggested that they are confamilial, in which case the name Triforinae would replace Cerithiellinae as it is the older name. However, since we include Cerithiellinae within the Cerithiopsidae we do not recognise Triforidae as a separate family. Little is known of Australian taxa allied to *Triforis*. Marshall (1977a) recorded nine Recent species in the genus, five (possibly six) of which are from New Zealand. The two known Australian species are *Triforis epallaxa* and *T. dexta*, both from South Australia.

Houbriek (1987d) recently described a new, large *Ataxocerithium* species from off New South Wales and Loch (1992) has reviewed the Australian members of that genus. Several genera recorded from the modern New Zealand fauna occur in Australia and are discussed by Marshall (1978). These include *Euselia*, *Cerithiopsis*, *Joculator*, *Holologica*, *Synthopsis*, *Prolixodens* and *Seila*.

Fossil species of the family are best known from the Eocene of the Paris Basin, from which Gougerot & Le Renard (1981) recognised 36 species. Fossils have been recorded from Australia, and the group is well represented in the Australian Tertiary (see Darragh 1970 for list of available taxa). Fossil of the family, however, are almost completely unworked.

Superfamily JANTHINOIDEA

Members of this small superfamily are carnivorous, feeding mainly on cnidarians. The group is characterised primarily by the presence of a ptenoglossate radula. This is a short, broad ribbon with numerous, uniformly arcuate or fang-like teeth that increase in size peripherally. The central tooth is often absent or greatly reduced. The radula (Fig. 15.151H) is set over the surface of the odontophore which is almost completely cleft into right and left halves by a mid-dorsal longitudinal groove. The radula differs from those of more typical gastropods in extending over the entire surface of the odontophore, even when within the buccal

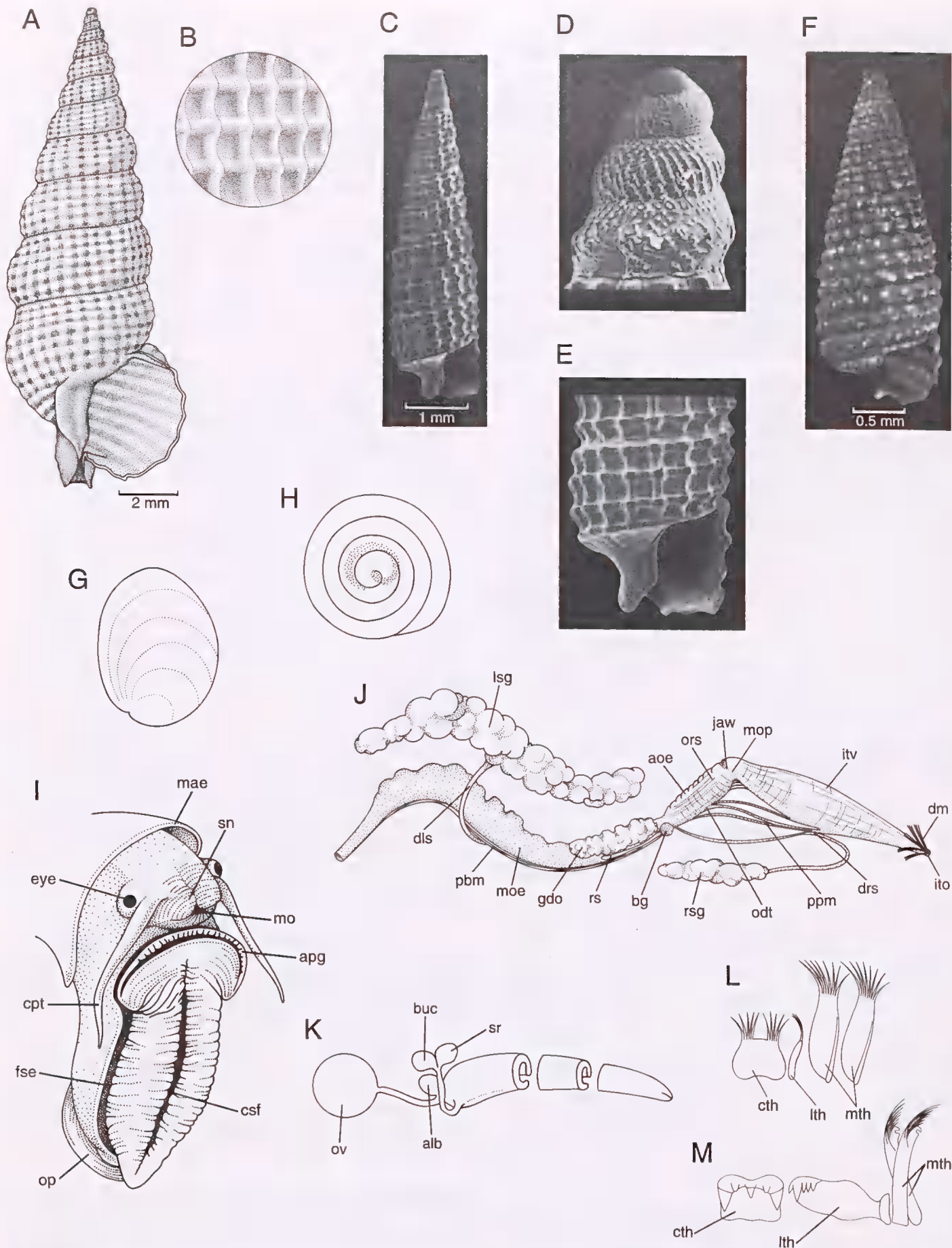


Figure 15.150 Family Cerithiopsidae. A, B, *Ataxocerithium serotinum*: A, shell, apertural view; B, shell sculpture. C-E, *Prolixodens infracolor*: C, shell, apertural view; D, protoconch; E, shell, last whorl and aperture. F, *Cerithiopsis carota*, shell, apertural view. G, H, opercula: G, *Prolixodens infracolor*; H, *Mendax trizonalis*. I, *Ataxocerithium eximium*, head-foot. J, *Cerithiopsis tubercularis*, anterior part of alimentary canal. K, *Cerithiopsis tuberculoides*, female genital duct. L, M, halves of a radular tooth row: L, *Mendax trizonalis*; M, *Seila terebelloides*. alb, albumen gland; aoe, anterior limit of anterior oesophagus; apg, anterior pedal gland; bg, buccal ganglion; buc, bursa copulatrix; cpt, cephalic tentacle; csf, longitudinal cleft in sole of foot; eth, central tooth; dls, duct of left salivary gland; dm, dilator muscles; drs, duct of right salivary gland; eye, eye; fse, furrow separating foot from sole; gdo, glandular diverticulum of oesophagus; ito, opening of introvert; itv, introvert; jaw, jaw; lsg, left salivary gland; lith, lateral tooth; mae, mantle edge; mo, mouth; moe, glandular wall of midoesophagus; mop, mouth position; mth, marginal teeth; odt, odontophore; op, operculum; ors, opening of right salivary duct into buccal cavity; ov, ovary; pbm, retractor muscles of proboscis; ppm, protractor muscles of proboscis; rs, radular sac; rsg, right salivary gland; sn, snout; sr, seminal receptacle. (C-F, from Marshall 1978; G, H, L, M, after Marshall 1978; I, after Houbbrick 1987d; J, after Fretter 1951b; K, after Houston 1985)

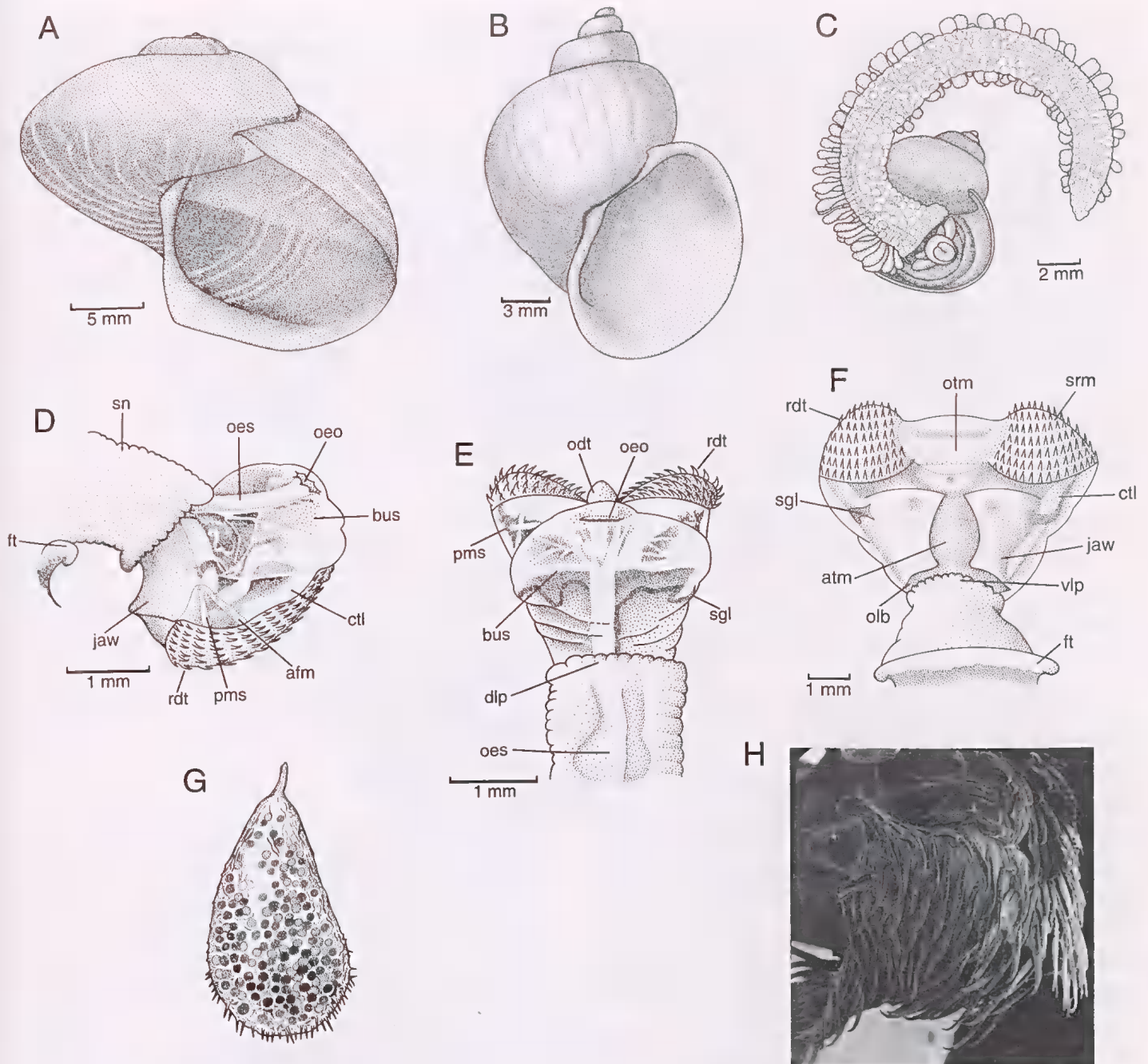


Figure 15.151 Family Janthinidae. **A, B**, shells, apertural view: **A**, *Janthina janthina*; **B**, *Recluzia rollandiana*. **C**, *Janthina exigua* as seen from above in its usual floating position, with egg capsules attached to the underside of the float. **D–F**, *Janthina janthina*, extrovert in feeding position: **D**, right lateral view; **E**, dorsal view; **F**, ventral view. **G**, *Janthina exigua*, egg capsule. **H**, *Janthina* sp., portion of radula. **afm**, accessory flexor muscle of the cartilage; **atm**, anterior transverse muscle; **bus**, buccal septum; **ctl**, cartilage; **dip**, dorsal lip; **ft**, foot; **jaw**, jaw; **odt**, odontophoral tip; **oeo**, opening of oesophagus on dorsal surface of extrovert; **oes**, oesophagus with underlying retractor muscle spreading into the buccal septum; **olb**, opening of labial gland; **otm**, outer posterior transverse muscle; **pms**, protractor muscle of the subradular membrane; **rdt**, radular tooth; **sgl**, salivary gland; **sn**, snout; **srm**, subradular membrane; **vlp**, ventral lip. (**C, G**, after Laursen 1953; **D–F**, after Graham 1965a)

cavity (Graham 1965a). In the Janthinidae, the walls of the buccal mass are everted through the mouth to form an extrovert. On protrusion the radula is spread laterally and its teeth are pulled erect. This constitutes the main feeding action, as on withdrawal of the extrovert the food is pulled into the buccal cavity. It is thought likely that all ptenoglossan radulae function in this way (Graham 1965a).

The ptenoglossate radula is present only in this superfamily and the related Eulimoidea (Haszprunar 1988a), but that group differs from the Janthinoidea in lacking paraspermatozoa (Healy 1988a). Characteristics of janthinoideans include paired salivary glands, usually with stylets at the openings to the salivary ducts, and the lack of a penis in many members (Thiele 1928b).

The superfamily consists of three ecologically divergent families, all of which occur in Australian seas. The family Janthinidae consists of exclusively pelagic species that feed on siphonophores. The Epitoniidae are a family of mainly burrowing species that feed

on anemones and corals. Representatives of both these families are common in Australian waters. The Aclididae are a small family of small to minute forms that appear similar to some eulimids in shell features. They are placed in this superfamily rather than the Eulimoidea mainly because of the radular structure and lack of a penis (Bouchet & Warén 1986; Ponder & Warén 1988).

This superfamily was known as the Epitonioidae, but the present name is used here, following Ponder & Warén (1988).

Family Janthinidae

The snails of this small, carnivorous, marine family are exclusively pelagic in habit and are cosmopolitan in tropical and warm temperate seas. They are commonly called violet snails as the most widespread and common genus, *Janthina*, has a thin, fragile, globosely trochiform violet shell. Most sustain themselves at the surface by constructing a mucous float of air bubbles. All of

15. PROSOBRANCHS

the five or six species now known from Australian seas were described from other tropical oceans before they were recorded from Australia. Bennett (1966) listed all the species recorded from Australian waters and described their associations with siphonophoran prey species and with other species of pelagic gastropods; he included references to all the earlier Australian records of the family. The spelling of the family and the nominate genus name here follow the original publication in using the initial 'J' rather than 'I' used by several modern workers following the monograph of the genus '*Janthina*' by Laursen (1953).

The shell is dextral, small to medium-sized (less than 25 mm in height), thin and fragile and composed almost entirely of calcite. It is turbiniform to globosely trochiform with a few convex whorls which are sometimes carinate, and has a low spire and no umbilicus (Fig. 15.151A, B). It is mainly smooth, but may have fine axial or spiral striae and is usually violet (*Janthina*) or more rarely white or brownish (*Recluzia*) in colour. There is no operculum. Species of *Janthina* have a slight to deep V-shaped central sinus in the outer lip and conspicuous chevron-shaped growth striae reflecting the form of the sinus.

The head is large, snout broad and the mouth terminal. In *Janthina* the animal is heavily pigmented (purple) and the bifid tentacles are black (Fretter & Graham 1962). Behind the tentacles is a stout, mobile neck that allows the animal to swing the head rapidly from side to side. No eyes are visible, but minute eyes, each complete with a lens, are present lying ventral to the cerebral ganglia under the muscles of the body wall posterior to the base of the tentacles.

The animals float at the surface with the foot uppermost by means of a bubble raft which spreads back from the mesopodium and rests on the surface film (Fig. 15.151C; Pl. 24.4). The foot is broad with an anterior, transverse furrow separating the propodium from the mesopodium. Along the centre of the anterior half of the mesopodium runs a groove (the funnel) into which the sole or pedal gland discharges mucus. The anterior end of the propodium traps a bubble of air from the surface and passes it back into the funnel where a skin of mucus forms around the bubble, hardening in contact with the water. The float attaches to the posterior end of the sole, the surface of which carries numerous longitudinal glandular ridges. Successive bubbles are pressed together, cemented by further secretions from the propodium, and formed into a tough structure of polyhedral bubbles. The float must be an important orientation organ as no statocysts or effective eyes are present.

The mantle cavity of *Janthina* contains a ctenidium, a large hypobranchial gland that produces a purple secretion, and a long, narrow osphradium. The buccal mass has a pair of jaws embedded in the anterior lateral walls. The floor of the buccal cavity is occupied by a large odontophore, with no clear radular sac, the radula being secreted in the posterior part of the cavity. A wide oesophagus opens from the dorsal part of the cavity. The radula is very complex, being a trough-like structure with steep sides, a deep cleft, and the floor incomplete. All the surfaces bear uniform curved, fang-like teeth (Fig. 15.151H). The radula is supported by a single cartilage. During feeding the buccal cavity is everted through the mouth to form an extrovert. The jaws come to lie on the underside, the radula at the extrovert's tip; the opening from the buccal cavity to the oesophagus forms a mouth-like aperture on its dorsal side. The radula is spread laterally and its teeth are erect (Fig. 15.151D–F). On retraction, the teeth fold over, pulling food into the buccal cavity. There are two pairs of tubular salivary glands which discharge into the buccal cavity. There are no oesophageal glands and no crystalline style (Fretter & Graham 1962; Graham 1965a). In *Recluzia*, the salivary glands lead to a pair of cuticular stylets surrounded by a sheath of muscle (Fretter & Graham 1962). The purple secretion from the hypobranchial gland may anaesthetise the prey to facilitate feeding (Hardy 1956). The animal feeds on the siphonophoran cnidarians *Veella*, *Physalia* and *Porpita*. Laursen (1953) also states that some species may feed on other janthinids as radulae have been found in gut contents, but this has yet to be confirmed.

Janthinids are protandrous hermaphrodites, but there is no penis in the male phase and no bursa copulatrix or seminal receptacle in the female phase. Graham (1954a) suggested that individuals undergo a sex change only once, but Laursen (1953) suggested that sex changes are repeated several times throughout life. Sperm transfer is by spermatzozeugmata. Active euspermatozoa are carried by the paraspermatozoa which facilitate the transport (Graham 1954a). Fertilisation occurs in the ovary.

Some species are ovoviviparous and others are oviparous – *Janthina exigua* and *J. pallida* produce egg capsules that they attach to the underside of the float. The capsules are pear-shaped, attached by a stalk and have a spiny surface (Fig. 15.151G). They are about 2 mm long and contain about 200 eggs per capsule in *J. exigua*, and are 4–7 mm long with 5000 eggs per capsule in *J. pallida*. All the eggs develop into larvae; there are no nurse eggs. Floats may have up to 250 capsules attached at all stages of development. On hatching, the young are liberated as veliger larvae. *Janthina janthina* is viviparous, retaining its eggs in the oviduct where they develop into veligers which are then liberated.

These snails are found in shoals or groups on the surface of the open ocean. Some shoals have been recorded as over 200 nautical miles across (Laursen 1953). Several janthinid species have been recorded in association with the three siphonophoran prey species listed above, together with other species of pelagic gastropods in the opisthobranch genera *Glaucus* and *Fiona*. These associations have been seen many times in Australian waters (Bennett 1966). A fossil genus, *Hartungia*, from the Pliocene–Pleistocene of southern Western Australia is referred to this family (Ludbrook 1978). *Hartungia* is also recorded from New Zealand, the Azores and Morocco as well as Australia; the genus has some stratigraphic value (see Ludbrook 1978).

Family Epitoniidae

This cosmopolitan family of marine carnivorous snails feeds almost exclusively on cnidarians. Epitoniids, unlike Janthinidae, are all benthic dwellers, often burrowing in the substratum; they range from intertidal waters to abyssal depths. The shells are usually high, conical, and many have a complex, fine sculpture of axial and spiral elements affording a beautifully moulded appearance. The group has the common name of 'wentletraps' from the German 'wendeltreppe' meaning a winding staircase (Pl. 24.6). Clench & Turner (1952) divided the family into two subfamilies, the Epitoniinae and Nystiellinae, on the basis of protoconch and radula structure. In the Epitoniinae, the nuclear whorls are smooth, shining and glass-like with no abrupt changes in whorl shape at the start of the post-nuclear whorls. The radular ribbon (Fig. 15.152D) is cap-shaped, narrowing anteriorly and posteriorly, but wide and folded in the centre. In the Nystiellinae, the nuclear whorls have strong axial sculpture with an abrupt change in whorl shape at the start of the post-nuclear whorls. In the genus *Solutiscula*, the only member of the subfamily examined, the radular ribbon is small, nearly equal in width for its entire length and has relatively few large, heavy, loosely attached teeth.

The shell is dextral, high conical to turret-shaped, rarely ovate-trochiform and almost entirely calcitic (Fig. 15.152A–C). It is small to medium in size, usually less than 30 mm and rarely to 100 mm in height. The spire is pointed with the protoconch often conical, frequently almost smooth and sometimes amber-brown in colour. Below this are about two whorls that are slightly dorso-ventrally flattened and sculptured with regularly spaced, sinuous axial growth lines that cross a subsutural spiral ridge, and faint spiral lines. Both these features are reminiscent of the *Janthina* protoconch (Robertson 1983a). The teleoconch whorls are mainly rounded, convex (though some species have flat-sided whorls for example, some *Opalia* species) and are either tightly or loosely coiled. Some groups have a peribasal cord that defines a 'basal disc' (for example, *Opalia* and *Cirsotrema*), but these are not present in *Epitonium*. At this point the sculpture may change: some genera (for example, *Opalia*) have a distinct intritacalx (P. Maxwell personal communication). The aperture is circular and often entire,

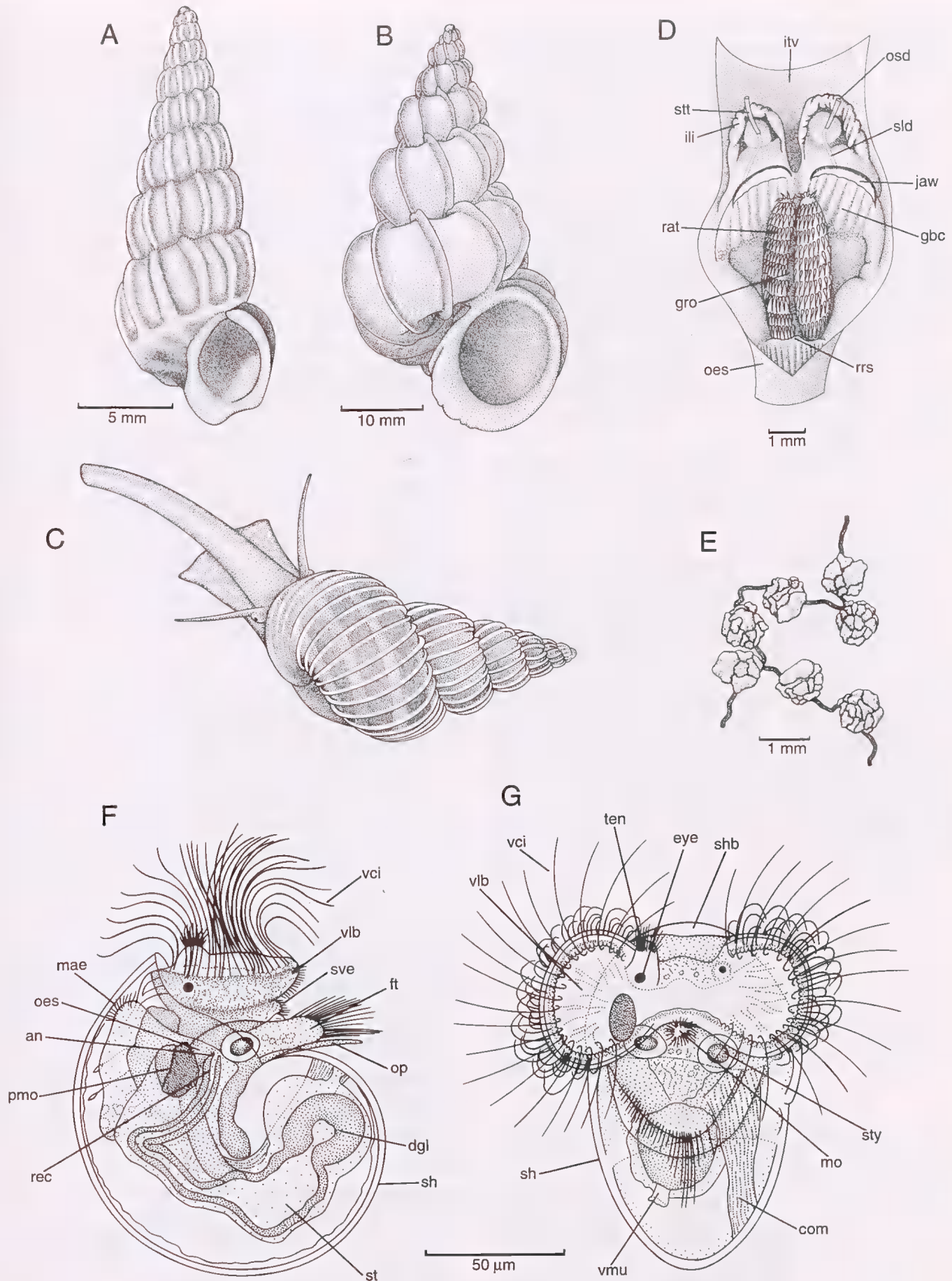


Figure 15.152 Family Epitoniidae. **A, B**, shells, apertural view: **A**, *Opalia consors*; **B**, *Epitonium scalare*. **C**, *Epitonium imperialis*, crawling animal. **D**, *Epitonium clathrus*, a mid-dorsal dissection showing the radula, the introvert, the buccal cavity and the anterior part of the oesophagus. **E**, *Epitonium jukesianum*, egg capsules. **F, G**, *Epitonium albidum*, newly hatched veligers: **F**, right lateral view; **G**, antero-ventral view. **an**, anus; **com**, columellar muscle; **dgl**, digestive gland; **eye**, eye; **ft**, foot; **gbc**, glands in wall of buccal cavity; **gro**, groove on mid-dorsal surface of buccal mass; **ili**, inner lip; **itv**, introvert; **jaw**, jaw; **mae**, mantle edge; **mo**, mouth; **oes**, oesophagus; **op**, operculum; **osd**, opening of salivary duct; **pmo**, pigmented mantle; **rat**, radular tooth; **rec**, rectum; **rrs**, roof of radular sac; **sh**, shell; **shb**, shell beak; **sld**, salivary duct; **st**, stomach; **stt**, stylet on which salivary duct opens; **sty**, statocyst; **sve**, subvelum; **ten**, tentacle; **vci**, velar cilia; **vlb**, velar lobe; **vmu**, velar muscle. (C, after Wilson & Gillett 1971; D, after Fretter & Graham 1962; E, after Smith, B.J., Black & Shepherd 1989; F, G, after Robertson 1983d) [C. Eadie]

15. PROSOBRANCHS

frequently with a thickened or doubled peristome. The umbilicus is present or absent depending on the tightness of the shell coiling. Sculpture is usually of axial and spiral elements, frequently of axial ribs, sometimes blade-like, which may be hooked at the shoulder or junction with the preceding whorl. The shell colour is usually white, sometimes banded or mottled in brown hues. The operculum is corneous, paucispiral to multispiral and light to dark brown with a central nucleus.

The head is narrow with long tapering tentacles bearing eyes at the outer bases (Fig. 15.152C). The foot is short and truncated anteriorly. The buccal mass is situated at the end of a long eversible (acrembolic) proboscis. There are two pairs of tubular salivary glands, one dorsal and one ventral. The dorsal pair open to the dorsal wall of the buccal cavity; the ventral pair have long ducts which expand into reservoirs and finally open through cuticular stylets which, in some species of *Epitonium*, arise from the centre of mammiform swellings lying, apparently external to the mouth, in a lateral position (Fig. 15.152D; Fretter & Graham 1962). The mantle cavity has a long narrow, finely bipectinate osphradium, a ctenidium and a hypobranchial gland that produces a purple secretion.

Epitoniids feed on cnidarians, primarily actinarian anemones and some corals. Feeding relationships of various species have been described as ranging from predacious to commensal or ectoparasitic according to the various interpretations put on the types of association between the various species and their prey (Robertson 1963b, 1980, 1983c, 1983d; Perron 1978). The radula is ptenoglossate, without a central tooth, but with series of uniform, usually arcuate, variously pointed (two to three cusps) teeth. Two pairs of tubular salivary glands are present; the oesophagus lacks oesophageal glands; and the stomach is large. Epitoniids are typically found burrowing in the substratum, often adjacent to an anemone or coral. Some are found exclusively in the company of one species of anemone whereas others have more varied dietary preferences. The feeding animal everts its proboscis and uses its radula and jaws to bite pieces off the prey; or some may swallow small anemones whole (Perron 1978). In the nervous system, the cerebral and pleural ganglia are very closely situated, the supra-oesophageal ganglion has connectives to both pleural ganglia and the suboesophageal ganglion is connected only with the left pleural.

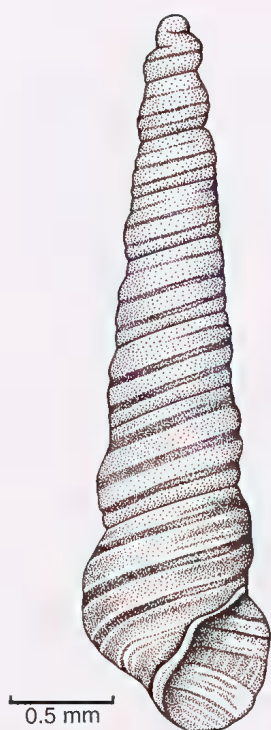


Figure 15.153 Family Aclididae. *Aclis* (Kimberia) *microscopica*, apertural view of shell. (After Hedley 1910a) [C. Eadie]

Epitoniids are protandric hermaphrodites. The male phase usually lacks a penis and has dimorphic sperm; the female phase has a receptaculum seminalis, albumen and capsule glands, and a slit-like gonopore. The assertion by Graham (1954a) that ptenoglossan spermatozeugmata swim from male to female is questioned following observations on *Epitonium albidum* by Robertson (1983d) and others: they pass from juxtaposed male to female in the ciliary water currents entering the latter's mantle cavity. This may be termed pseudocopulation, with the euspermatozoa then making their way to the ovary. Eggs are laid in elliptical, thick-walled capsules that are sand-agglutinated (Fig. 15.152E). Each capsule is attached on its side to an elastic, mucous thread that extends from one capsule to the next. The thread originates from the pedal mucous pore, not from the oviducal glands (Robertson 1983d). In some populations of *Epitonium albidum*, small females lay smaller capsules containing fewer eggs than larger females. In the small Australian species, *Epitonium jukesianum*, egg masses containing from 50–200 capsules have been observed. Each capsule is between 0.6–0.8 mm in diameter and hatching takes place about eight days after laying, with a break in the capsule wall through which the veligers emerge (Smith, Black & Shepherd 1989). From a study of the protoconch, it is thought that the veligers (Fig. 15.152F, G) are pelagic and planktotrophic with a long stay in the plankton ensuring wide dispersal. For *Epitonium millicostatum*, Robertson (1980) estimated that the planktonic stage lasts at least a month. One or two species in the family are reported to have direct development without a planktonic larva, for example, *Epitonium greenlandicum* from the north-eastern Atlantic (Bouchet & Warén 1986). Robertson (1983b) studied the postlarval growth of *Epitonium albidum*.

The family is very diverse, comprising several hundred species worldwide in 30–40 genera and subgenera (about 100 nominal genera have been proposed, the status of many of which is unknown). Important recent revisions of sections of the world fauna include those of Kilburn (1985) and Bouchet & Warén (1986). Iredale (1936a) and others have proposed many generic and species names for Australian epitoniids; many species may be endemic. There has, however, been no comprehensive list or revision of the Australian fauna and the taxonomy unclear. At present Australian species are referred to several genera, most of which are cosmopolitan: *Epitonium*, *Cirsotrema* and *Opalia*, sometimes with subgenera. Works on parts of the Australian fauna include those of Iredale (1936a), Cotton (1956), Iredale & McMichael (1962), Macpherson & Gabriel (1962) and Cernohorsky (1972). Many of the forms from tropical Australia have a wide, Indo-Pacific distribution, whereas some species from southern Australia appear to be endemics (Wilson & Gillett 1971). Vaught (1989) and Wilson (1993) listed several subgenera of *Epitonium sensu lato* that may be applied to Australian endemic species. These include *Foliaeiscala*, *Globiscala*, *Hirtoscala*, *Laeviscala*, *Lamelliscala* and *Limiscala*.

Epitoniids are recorded as fossils from the Tertiary of Victoria and South Australia (Ludbrook 1957). A sinistral species in a new genus, *Kallosinistrala*, which may be referable to this family, has recently been described from the Eocene of Seymour Island, Antarctica (Stilwell & Zinsmeister 1992).

Family Aclididae

This is a small family with mainly minute, high-spired shells (mostly under 5 mm in length) about which very little is known. A report on species from the North East Atlantic by Bouchet & Warén (1986) mentions that Warén is currently undertaking a worldwide revision of the family. Preliminary results from this work indicate that of the numerous genera formerly included in the family, only *Aclis* will remain.

Typical species of *Aclis* have shells with one or several strong spiral keels, and a flaring outer lip; they are tall and *Turritella*-shaped (Fig. 15.153). The protoconch is smooth and the aperture has a distinctly reflected inner lip with a narrow umbilical chink, an

opisthocline outer lip and the lower part of the aperture drawn out towards the centre of the shell and distinctly flattened. The shells are vitreous and transparent though variable in shape and sculpture.

Little is known of the anatomy of the group as very few specimens have been observed alive. Sars (1878) figured the ptenoglossate radula and Bouchet & Warén (1986) reported a large pedal fold on each side of the foot in *A. minor*, covering the base of the shell when the animal is crawling. The male appears to have no penis. Nothing is known of the general biology of the family.

Several genera and species of Australian molluscs have been referred to this family, only to be assigned later to other families (Garrard 1972; Ponder 1974). *Cyclonoidea* is considered a synonym of *Aclis* by Bouchet & Warén (1986) with *C. carina* from northern Australia as its type species. The Australian genus *Coenaculum*, erected by Iredale (1924), has been referred to this family (Ponder 1985a), but probably belongs elsewhere (W.F. Ponder personal communication).

Superfamily EULIMOIDEA

This group of parasitic gastropods was revised by Warén (1983a). He united the former families Eulimidae, Stiliferidae, Entoconchidae, Asterophilidae and Enteronidae into the single family Eulimidae in the superfamily Eulimoidea. He suggested that the family Aclididae should also be placed in this superfamily, but Ponder & Warén (1988) transferred that family to the Janthinoidea. The Eulimoidea are separated from the Janthinoidea mainly on the basis that they lack paraspermatozoa (Healy 1988a). They have a penis, lack purple hypobranchial secretion and have a closed pallial genital duct (see Warén 1983a). The characters of the superfamily are those of the family.

Family Eulimidae

Species in this large marine family are parasitic, mostly on echinoderms (Pl. 24.5). Many are ectoparasites more or less permanently attached to their host by the snout or proboscis, but some are highly modified endoparasites showing major anatomical reductions and transformations associated with the parasitic mode of life. Earlier workers have used the many differences in shell and anatomy to divide the group into various family and superfamily groupings (for example, Laseron 1955). These differences, however, have been shown to be specialisations connected with the degree of parasitism of the particular species and more recent work has shown that this wide variation still falls within the bounds of one family (Ponder & Gooding 1978; Warén 1983a).

The shell is usually present (absent in the most specialised endoparasites) and varies in shape from high-spined, long, narrow and slightly curved to inflated, globose and even patelliform as in *Thyca* species (Fig. 15.154A–F). Most primitive species have a straight conical shell with flat whorls, a polished surface and a high spire. Many species have coloured shells, some marked with brownish bands or spots on a yellow background; the presence of colour, however, is not a good feature for generic discrimination. The shell is usually small (most being less than 5 mm in length), and rather solid. The suture is very shallow and marked by a less transparent spiral band and in many species is quite indistinct. In most eulimids, the shell surface is smooth although many appear to have fine spiral or axial striae, a refractive phenomenon caused by the crystalline structure of the calcium carbonate. Some species have quite prominent sculpture. Almost all eulimids have scars from earlier positions of the outer lip formed by growth; in some this is quite regular. Two genera, *Niso* and *Microstilifer*, have an umbilicus. An operculum is present in all species with solid shells, and sometimes has a peg, folds or other reinforcement. It is lacking in species that are constantly attached to the host and have inflated or less solid shells.

Morphology is highly variable within the family, probably due to specialisations for parasitism. In the less modified (or primitive) types, such as *Eulima*, *Melanella* or *Vitreolina*, the foot is long and slender with a well-developed propodium (Fig. 15.154J, K).

The posterior pedal gland, which secretes a thin mucous thread that the animal uses to attach itself to the host, opens in the centre of the sole. The anterior pedal gland opens at or just behind the proboscis opening and in many species is an extremely large gland (Fig. 15.154K). In *Vitreolina*, the head is protected by the shell when the animal is crawling, with only the tentacles and the anterior part of the foot protruding (Fig. 15.154J). A pair of eyes is situated basally, under the skin in the centre of each tentacle. The eyes have a lens, and are present in most species, including many abyssal species and those that live in galls or as endoparasites. The proboscis opening is usually situated under the tentacles, but in many sedentary species there is a snout and the opening is situated in its centre (Fig. 15.154G, J). The parasite usually attaches to the host by its snout, as in *Echineulima* (Lützen & Nielsen 1975); however, in some species it is transformed into a sac-like structure, the pseudopallium, which covers the base of the shell (Fig. 15.154I). The pallial cavity usually contains a ctenidium, osphradium and hypobranchial gland, and a pallial tentacle has been reported in *Eulima* (Warén 1983a).

In a presumed primitive or unmodified form, there is a simple acrembolic proboscis, with a muscular sheath. The radula is ptenoglossate. In *Niso* the radula has about 45 rows of flat, bicuspidate teeth; in *Eulima* it has fewer unicuspidate teeth; and in *Hemiliostraca* about 20 rows of more needle-shaped teeth are present. Also in *Hemiliostraca* there are two semi-circular jaws equipped with needle-shaped teeth along the curved margin. The lumen of the oesophagus is lined with cuticle, as in the Epitoniidae. *Eulima* has a pair of salivary glands lying directly behind the buccal mass in front of the nerve ring, whereas in other genera these glands are very long, lying along the oesophagus. The alimentary system is extensively modified in various ways in the species adapted to a more parasitic mode of life.

In many eulimids, sexes are separate and there is pronounced sexual dimorphism with males being 0.1–0.7 times the size of females (Fig. 15.154H). Other species are protandric hermaphrodites, and in many genera there is environmental sex determination. A number of species are simultaneous hermaphrodites (all ectoparasites). Some are permanently attached and are always found in couples. A penis is present in all species, except those which have internal dwarf males. The pallial vas deferens opens into the pallial cavity. In females, the pallial oviduct and the capsule gland are open in the mantle cavity. Details of the life histories of several species have been described by Lützen (1972, 1976). In *Pelseneria brunnea*, a parasitic species on the common purple sea-urchin, *Heliocidaris erythrogramma*, in south-eastern Australia, several individuals occur together, attached to the centre of the aboral surface, each with its long proboscis inserted through a hole in the test. Small balloon-shaped egg capsules are attached to the test by a short stalk. Each capsule is about 0.75 mm in diameter and contains 20 to 30 spherical white eggs each about 0.2 mm in diameter. Up to 40 capsules at all stages of development have been seen on one urchin. Juveniles hatch as crawling miniature adults (Smith, Black & Shepherd 1989).

The extent of the Australian fauna is unknown as the status of many of the nominal species in the literature must be questioned in light of recent work. More modern work on the fauna includes that by Lützen (1972, 1976); Lützen & Nielsen (1975); Ponder & Gooding (1978), Warén (1980a, 1980b, 1981a, 1981b, 1983a) and Bouchet & Warén, (1986). A recent listing of genera (with the number of species thought to occur in Australia) is as follows (Wilson 1993): *Apicalia* (four), *Asterolamia* (one), *Curveulima* (one), *Echineulima* (three), *Eulima* (13), *Eulitoma* (one), *Fusceulima* (five), *Hebeulima* (seven), *Hemiliostraca* (one), *Hypermastus* (six), *Leutzenia* (one); *Megadenus* (one), *Melanella* (10), *Microstilifer* (one), *Mucronalis* (two), *Paramegadenus* (two), *Parvioris* (six), *Peasistilifer* (two), *Pelseneria* (one), *Sabinella* (one), *Sticteulima* (one), *Stilapex* (five), *Stilifer* (five), *Scalenostoma* (one), *Thyca* (three), *Trochostilifer* (one) and *Vitreobalcis* (one). Many species names are known from the Tertiary of Australia, but again their status needs re-evaluation.

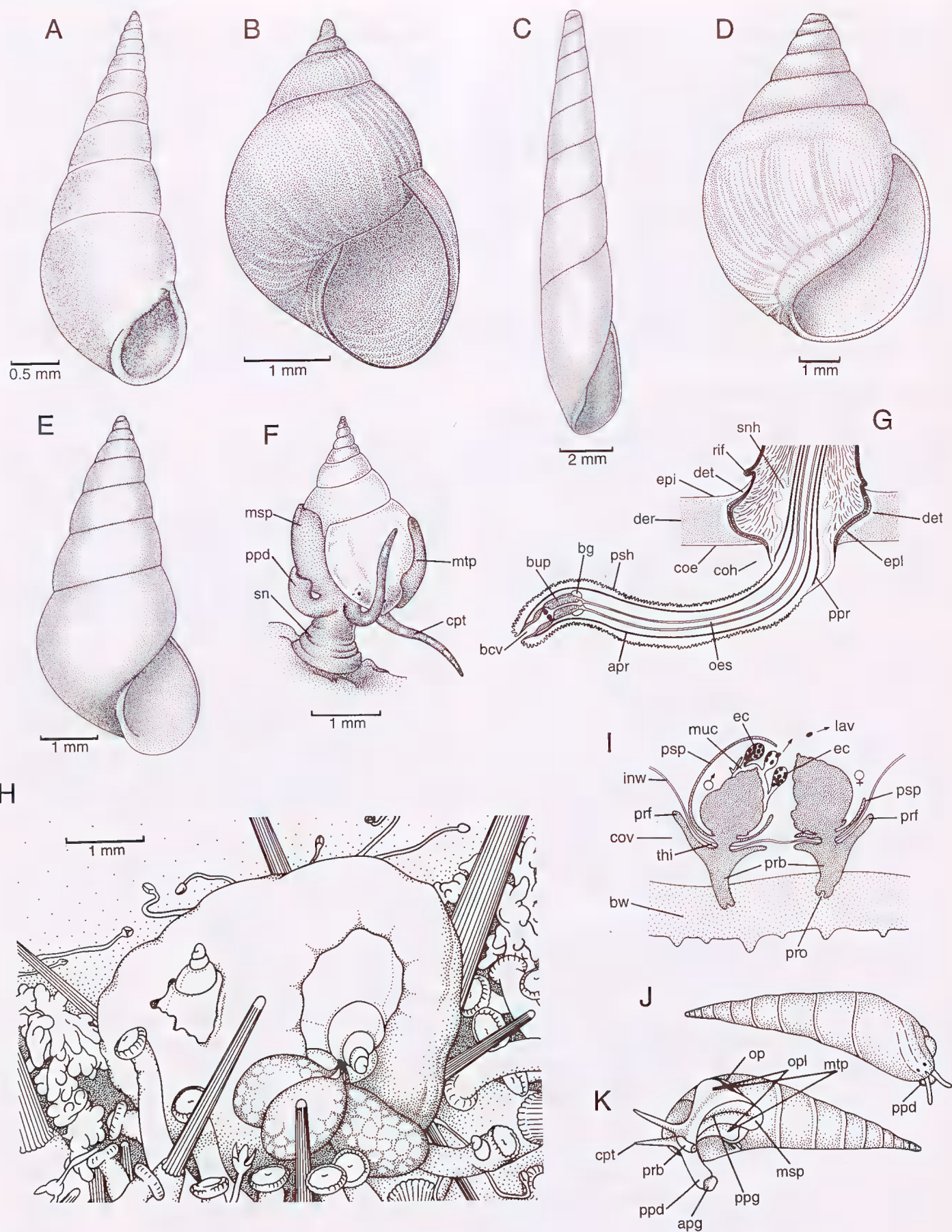


Figure 5.154 Family Eulimidae. A–E, shells, apertural view: A, *Melanella schoutamica*; B, *Pelseeneeria brunnea*; C, *Eulima acutissima*; D, *Stilifer inflatus*; E, *Apicalia brazieri*. F, G, *Echineulima mittrei*: F, live animal attached to a sea urchin; G, diagram of snout and everted proboscis. H, *Monogamus entopodia*, male and female with egg capsules, in a transformed tube foot of a sea urchin. I, *Megadenus cantharelloides*, position in the intestine of a host (holothurian). J, K, *Vitreolina philippii*, general appearance of the body of a primitive eulimid: J, dorsal view; K, ventral view. **apg**, anterior pedal gland; **apr**, anterior proboscis retractor; **bvc**, buccal cavity; **bg**, buccal ganglion; **bup**, buccal pump; **bw**, buccal wall of host; **coe**, coelomic lining of testis; **coh**, coelom of host; **cov**, coelomic cavity of host; **cpt**, cephalic tentacle; **der**, dermis of test; **det**, transformed zone of dermis lacking endoskeleton; **ec**, egg capsule; **epi**, epidermis of test; **epl**, epithelium of snout specialised for attachment; **inw**, intestinal wall of the host; **lav**, larva; **msp**, mesopodium; **mtp**, metapodium; **muc**, mucous layer covering the male shell; **oes**, oesophagus; **op**, operculum; **opl**, operculigerous lobe; **ppd**, propodium; **ppg**, posterior pedal gland; **ppr**, posterior proboscis retractor; **prb**, proboscis; **prf**, proboscis fold; **pro**, proboscis opening; **psh**, proboscis sheath; **psp**, pseudopallium; **rif**, ring fold; **sn**, snout attached to sea urchin test; **snh**, snout haemocoel (with reservoirs almost emptied); **thi**, thickening. (F, G, after Lützen & Nielsen 1975; H, after Lützen 1976; I–K, after Warén 1983a)

Infraorder NEOGASTROPODA

The Neogastropoda underwent a remarkable radiation in the Cretaceous and early Cainozoic (Ponder 1973a; Taylor, J.D. & Morris 1988), presumably after the adoption of a carnivorous diet. Ponder (1973a) recognised within this large group of mainly carnivorous gastropods the following groups: the Muricoidea – equal to Thiele's (1929–1935) Muricacea + Buccinacea + Volutacea (excluding Cancellariidae), the Cancellarioidea and the Conoidea (= Toxoglossa). These separate groups were based primarily on differences in foregut structure, including the radula. A full listing of family group names was provided by Ponder & Warén (1988). However, there is now evidence that at least one of these groupings (Muricoidea *sensu* Ponder 1973a) is probably paraphyletic. For example, in what was considered to be one family alone (Olividae), Kantor (1991) has recognised three families which he places in two separate 'suborders'. In addition, molecular data appear to indicate that the Muricoidea is paraphyletic to the Cancellarioidea (see under Cancellarioidea below). Because the modifications to Ponder's (1973a) classification are currently unsettled, it has been maintained in this volume. Since this account was written, Kantor (1996) has proposed additional modifications to neogastropod phylogeny and classification.

Among neogastropods a number of autapomorphies can be identified, assumed to be derived secondarily and therefore not synapomorphic. These derived character states include (Ponder 1973a) a rachiglossate or toxoglossate radula, a gland and valve of Leiblein (or, in the conoideans, its homologue the poison gland), anal (or rectal) gland, accessory salivary glands (see also below under the detailed treatment of the contained superfamilies). Whereas it has been assumed (for example, Ponder 1973a) that the anal gland and accessory salivary gland were lost in buccinids and related groups, an alternative possibility is that their absence is plesiomorphic (Ponder & Lindberg 1997). This latter contention is supported by the primitive condition of the stomach (presence of a caecum) in buccinids and related taxa compared with many other neogastropods (Smith, E.H. 1967b; Medinskaya 1993). The structure and function of the neogastropod anal (= rectal) gland (Schaefer 1996) was described by E.B. Andrews (1992). It extracts cations and macromolecules from the blood and is involved in metabolism. The gland also houses symbiotic bacteria. The absence of this gland in some neogastropods (Fretter & Graham 1962; Ponder 1973a) is correlated with a reduction in the size of the rectal sinus and an increase in renal complexity (Andrews, E.B. 1992).

The identity of the sister taxon of the Neogastropoda continues to be a matter for speculation (for example, Ponder 1973a; Shimek & Kohn 1981; Healy 1988a; Taylor, J.D. & Morris 1988). Ponder (1973a) suggested that the Neogastropoda was derived from 'archaeogastropods' or primitive 'mesogastropods', contrary to the previously held view that it was derived from 'higher mesogastropods', notably from the Tonnoidea. Haszprunar (1985a) demonstrated convincingly that the Caenogastropoda could be defined by an autapomorphic histology of the osphradium (presence of Si cells) and Healy (1988a) noted that neogastropods and 'higher mesogastropods' (*i.e.* the Hypsogastropoda) have similar sperm morphology, particularly sharing a similar type of parasperm. A ventral pedal gland for moulding egg capsules is also shared with some Velutinoidea and Tonnoidea, in the Hypsogastropoda. Thus, there seems little doubt that the sister group to the Neogastropoda lies within the Hypsogastropoda.

Superfamily MURICOIDEA

The Muricoidea is a large and diverse, worldwide superfamily of mainly marine snails possessing a pleurembolic proboscis, and a rachiglossate radula, and typically having two pairs of salivary glands, an anal (or rectal) gland, and a gland and valve of Leiblein in the anterior gut. The superfamily, as recognised here, includes three superfamilies recognised by Thiele (1929–1935), the

Muricacea, Buccinacea and Volutacea. These three superfamily groupings were based on a few superficial similarities, mainly in shell and radular characters, and were combined by Ponder (1973a), although the old superfamily names are still often used. The following account is based largely on information contained in Ponder's (1973a) review of the Neogastropoda. Work undertaken in the last few years by a number of authors including Y.I. Kantor, M.G. Harasewych and J.D. Taylor has provided a great deal of additional data strongly indicating that this classification requires considerable modification (see also below). However, results to date are not sufficiently clear-cut to adopt a new classification so we have maintained Ponder's (1973a) conservative classification.

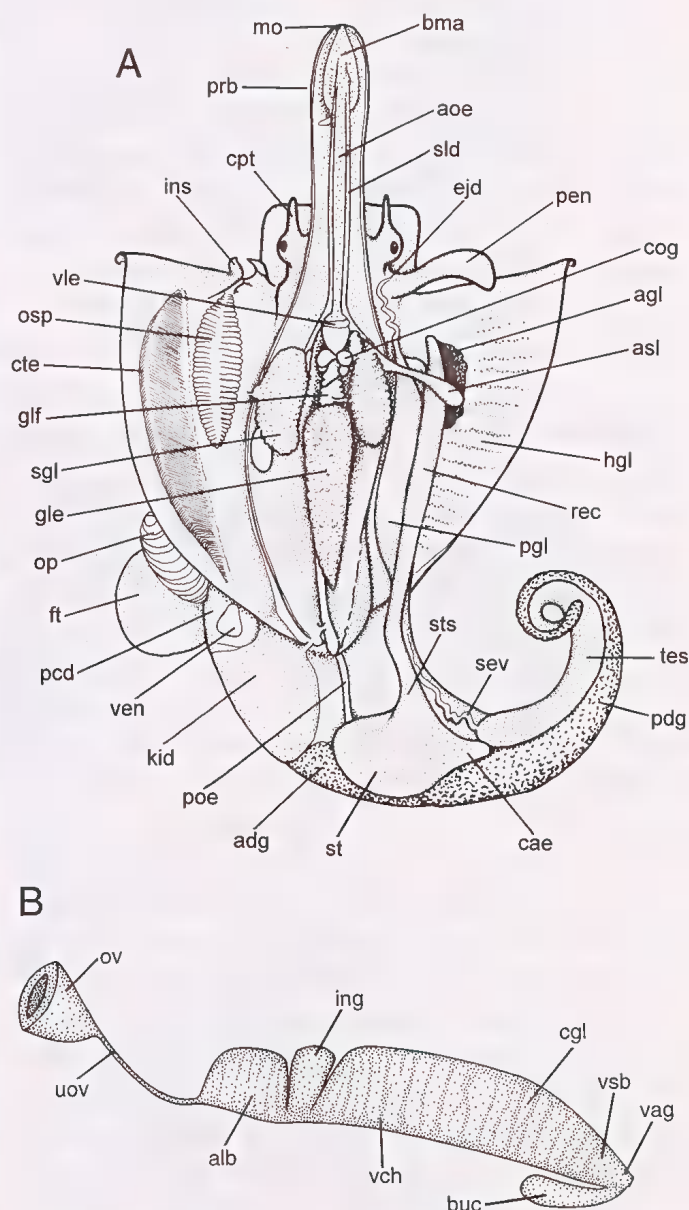


Figure 15.155 Superfamily Muricoidea. **A**, a muricoidean neogastropod removed from its shell, dorsal view, with the proboscis extended and the mantle cavity and anterior body cavity opened mid-dorsally. **B**, a generalised neogastropod oviduct, right lateral view. **adg**, anterior lobe of digestive gland; **agl**, anal gland; **alb**, albumen gland; **aoe**, anterior oesophagus; **asl**, accessory salivary gland; **bma**, buccal mass; **buc**, bursa copulatrix; **cae**, gastric caecum; **cgl**, capsule gland; **cog**, circumoesophageal ganglia; **cpt**, cephalic tentacle; **cte**, ctenidium; **ejd**, ejaculatory duct; **ft**, foot; **gle**, gland of Leiblein or foregut gland; **glf**, glandular dorsal folds of mid-oesophagus; **hgl**, hypobranchial gland; **ing**, ingesting gland; **ins**, inhalant siphon; **kid**, kidney; **mo**, mouth; **op**, operculum; **osp**, osphradium; **ov**, ovary; **pcd**, pericardium; **pdg**, posterior lobe of digestive gland; **pen**, penis; **pgl**, prostate gland; **poe**, posterior oesophagus; **prb**, proboscis; **rec**, rectum; **sev**, seminal vesicle; **sgl**, salivary gland; **sld**, salivary duct; **st**, stomach; **sts**, style sac region of stomach; **tes**, testis; **uov**, upper oviduct; **vag**, vagina; **vch**, ventral channel; **ven**, ventricle; **vle**, valve of Leiblein; **vsb**, vestibule. (**A**, **B**, after Ponder 1973a) [A, M. Thompson; B, C. Eadie]

15. PROSOBRANCHS

Muricoidean shells are typically elongate fusiform to ovate, rarely sub-patelliform in shape, with an elongate to involute spire. They have an anterior siphonal channel or canal, and are smooth to elaborately sculptured. Larval development (and hence protoconch morphology) is diverse. An operculum is present or absent, when present it is horny, rarely coiled and variable in shape and sculpture, between, and even within families.

The general anatomy of a muricoidean is illustrated in Figure 15.155A. The head has a pair of cephalic tentacles, typically with the pair of eyes in swellings or peduncles some distance from their bases. An inhalant siphon is always present and is often long and may or may not be protected by a siphonal canal of the shell. No accessory tentacles are developed from the mantle edge or the foot, except in nassariids which have two posterior pedal tentacles. The foot is small to large relative to the shell, with or without an antero-ventral capsule-moulding gland in females and in many muricids has an accessory boring organ. An anterior pedal gland is present. A large bipectinate osphradium is found in all neogastropods, and the ctenidium is well developed and usually extends most of the length of the mantle cavity. Much of the posterior two thirds of the mantle roof to the right of the ctenidium is occupied by a well-developed hypobranchial gland. The hypobranchial secretion is sometimes coloured, the chemicals in some groups changing colour when exposed to light. A small to large, usually darkly pigmented anal gland, with a narrow duct to the distal part of the rectum, is present in most families, lying on the left side of the rectum.

Most muricoideans are carnivores, although, secondarily, a few have become omnivores, deposit-feeders or herbivores. Feeding methods vary from active prey-seeking (the prey mainly polychaetes and molluscs) to grazing on colonial animals (for example, some marginellids and coralliophilines) to scavenging and omnivory (for example, some buccinids) to detritus-feeding (for example, some Buccinidae (Nassariinae) and herbivory (for example, some columbellids) (see Taylor, J.D. *et al.* 1980 for a summary). Muricids actively bore holes in the shells of their prey (see review by Kabat 1990a) and members of at least one genus in the Marginellidae (Ponder & Taylor 1992) and Buccinidae (Peterson & Black 1995) can also bore. The anterior alimentary canal is dominated by a pleurembolic proboscis which may be short, not much longer than the buccal mass, to very long and narrow with the proboscis sac filling most of the cephalic haemocoel. A pair of lateral jaws is present and the radula is rachiglossate (1–1–1 or 0–1–0) or is absent. The teeth usually bear simple, sharp cusps and often have simple bases. The salivary glands are paired and one or a pair of accessory salivary glands is often present (but absent in Buccinidae and Columbellidae). The anterior oesophagus is usually long and simple, terminating at the valve of Leiblein which lies on the anterior side of the nerve ring. This is the beginning of the mid-oesophagus and typically is dominated by a large gland of Leiblein, which is in part a modified oesophageal gland. This gland is separate from the oesophagus, joined only by narrow duct, and may be broadly triangular in shape ranging to elongate or may even be a long coiled muscular tube resembling the poison gland of toxoglossans (Ponder 1970a, 1973a), or rarely, may be absent (for example, in the Harpidae). The stomach is rather simple in most carnivorous groups, but in a few (some Nassariinae, Buccinidae) a crystalline style is present. A caecum may or may not be present. The kidney either has the renal lamellae interdigitated (méronephridien) or in two separate areas (pyncnonéphridien) (Perrier 1889), nearly all families having only one type or the other (Ponder 1973a).

The nervous system is typical of higher caenogastropods, usually showing considerable concentration of the ganglia (summary and references given by Ponder 1973a).

The female reproductive system (Fig. 15.155B) typically consists of an ovary located in the visceral spire, more or less separated from the digestive gland; a thin-walled upper oviduct; a short renal oviduct, often with a gono-pericardial canal, and a glandular section which consists of a posterior albumen gland and an anterior capsule

gland. A sac lined with columellar epithelium, the ingesting gland, lies between these two glands and often there is an anterior bursa copulatrix and a posterior seminal receptacle, the latter derived from the renal oviduct. There is often a gland in the anterior sole of the foot which is utilised for moulding the egg capsules. Males have a testis in the same position as the ovary, but often larger. The vas deferens expands to form a seminal vesicle and the renal part sometimes has a gono-pericardial duct (Fretter & Graham 1962), a character not seen in neotaenioglossans. The prostate gland is more or less pallial and may be open or closed, sometimes with a posterior vent. The anterior vas deferens is an open groove or a closed tube, sometimes a muscular ejaculatory duct, and the penial duct shows a similar range of variation. The penis is located behind the right eye and is variable in form, often being diagnostic at the species level. Sperm are dimorphic and similar to those of some neotaenioglossans in having simple parasperm (Healy 1988a). Larval development either includes a veliger stage or is direct. Direct developers utilise nurse eggs, albumen or yolk, depending on the group. Egg capsules are very variable in shape from group to group and within groups, ranging from lens-shaped or hemispherical (probably the primitive state) to vase-shaped or grouped into complex masses.

The Muricoidea is a very large superfamily, having considerable importance ecologically and commercially. Some muricoideans are pests (for example, oyster drills – Muricidae; Pl. 27.4), others are used as food (for example, whelks – Buccinidae) and many have considerable value as collectors items (for example, many volutes). Others are abundant, especially in low tidal to sublittoral marine ecosystems (for example, some species of *Cominella* in Australia and New Zealand, and *Nassarius* in many parts of the world). Muricoidea live mainly in shallow marine ecosystems throughout the world. Some are found in the deep sea (for example, most Columbariinae, family Turbinellidae) and inhabit virtually all possible benthic microhabitats. Species in one genus, *Clea* (Buccinidae), live in freshwater.

The number of families recognised has not yet stabilised. The group is a relatively recent one, first appearing about 100 mya in the Albian (lower Cretaceous) and then undergoing an explosive radiation (Ponder 1973a; Taylor, J.D. *et al.* 1980; Taylor, J.D. & Morris 1988). The boundaries between some previously recognised family units are not clear cut (for example, between the Buccinidae, Nassariidae and the Fasciariidae) and Ponder (1973a) suggested that these families should be regarded as a single unit. This proposal was accepted formally by Ponder & Warén, in 1988, who recognised 11 Recent families, all of which are found in Australia. Since then, a new family (Pleioptygmatidae) has been proposed by Quinn (1989) for a Caribbean species, and Kantor (1991), on the basis of detailed anatomical studies, has split the Olividae into several families assigned to three superfamilies and two suborders. It seems that the monophyly of the Muricoidea as recognised here is not supported. More detailed anatomical and cytological work supported by molecular studies will no doubt help to resolve this in the future. The question of rank, however, will always be arbitrary. The conservative approach favoured by Ponder (1973a) and Ponder & Warén (1988) and used here does have the disadvantage of hiding relationships in a classification involving few levels. Alternative schemes that have been proposed (for example, Golikov & Starobogatov 1975) are usually not acceptable because they are supported by insufficient data. In contrast, Kantor's (1991) work on 'oliviform' gastropods and his more recent re-analysis of neogastropod phylogeny (Kantor 1996) are, perhaps, the starting point of a new direction in neogastropod classification as distinct from any debate that might be held over the ranks given to higher taxa.

Family Muricidae

Muricids are an important group of marine predatory snails. They have small to large-sized, highly variable shells that are rarely smooth, usually being elaborately sculptured with spiral and axial sculpture. The shells typically have prominent varices, which often bear nodules or spines, and the anterior siphonal canal is

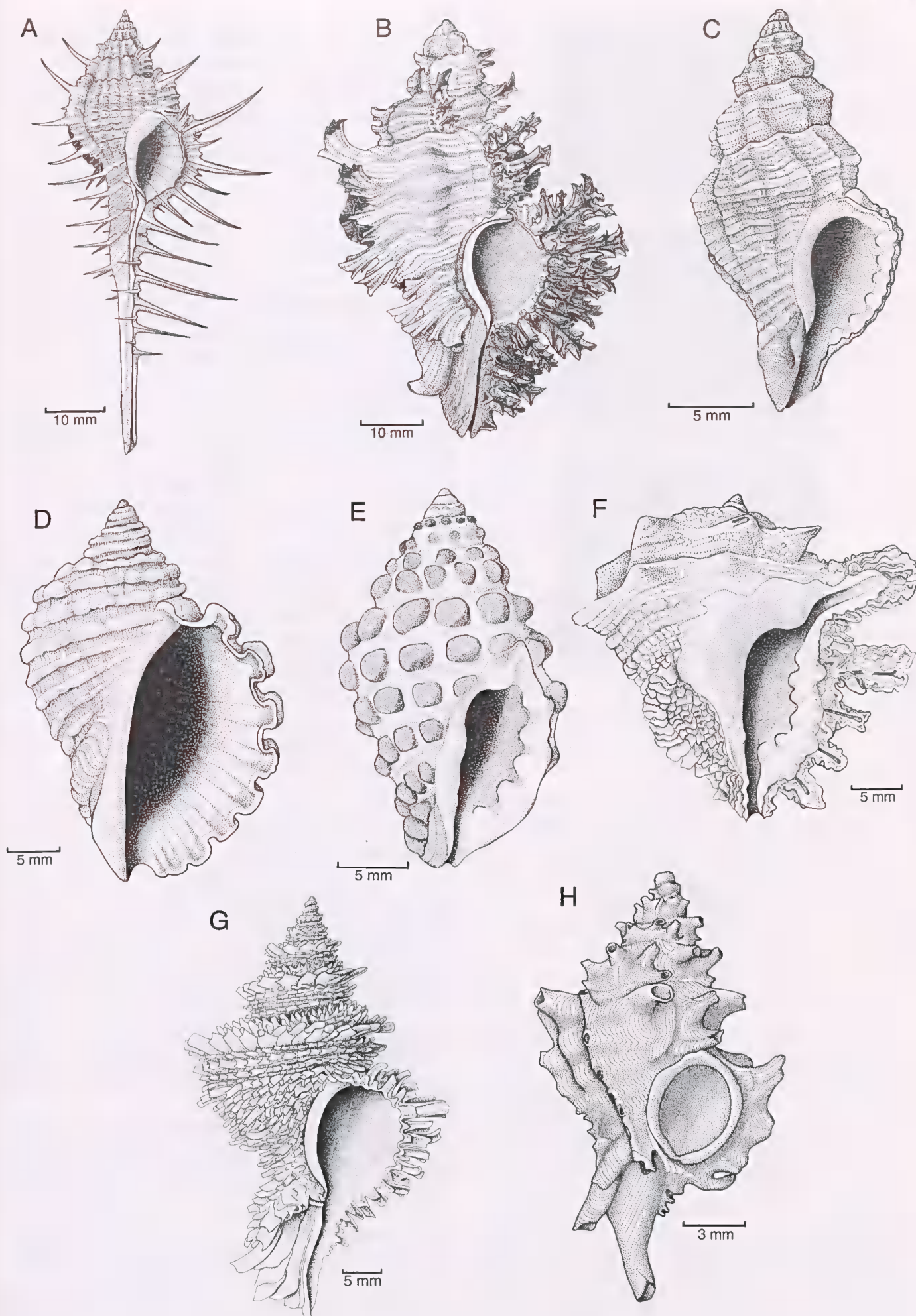


Figure 15.156 Family Muricidae. A–H, shells, apertural view: A, *Murex queenslandicus*; B, *Chicoreus brunneus*; C, *Bedeva hanleyi*; D, *Dicathais orbita*; E, *Morula granulata*; F, *Drupa grossularia*; G, *Babelomurex lischkeanus*; H, *Typhis philippensis*. [A–G, S. Weidland; H. C. Eadie]

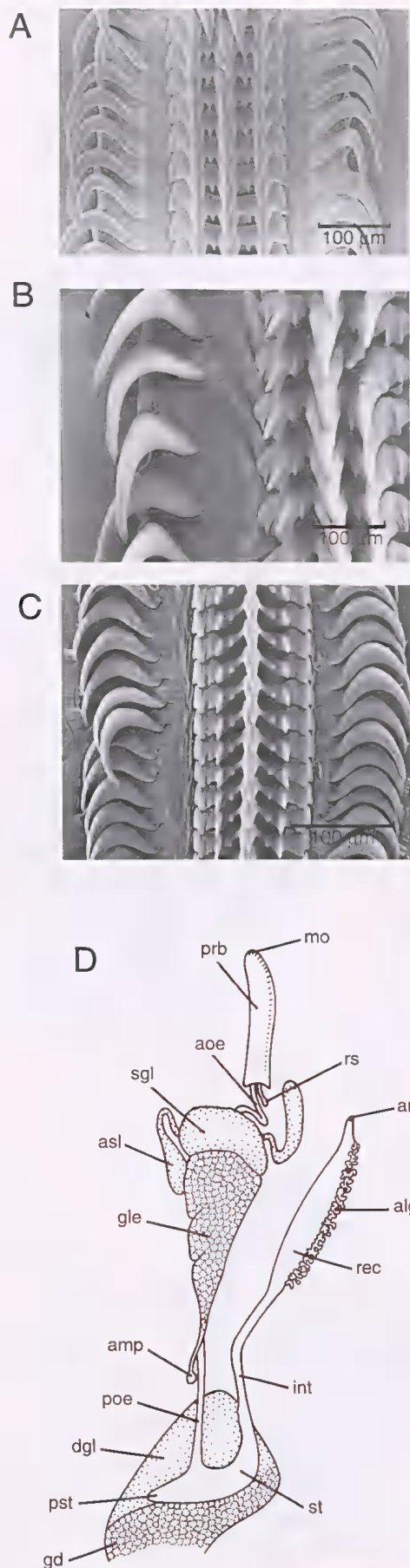


Figure 15.157 Family Muricidae. A–C, portions of radulae: A, *Chicoreus cornucervi*, a number of transverse rows; B, *Dicathais orbita*, teeth on one side; C, *Morula marginalba*, a number of transverse rows. D, *Drupa ricina*, digestive system, dorsal view. anl, anus; alg, anal gland; amp, ampulla; aoe, anterior oesophagus; asl, accessory salivary gland; dgl, digestive gland; gd, gonad; gle, gland of Leiblein; int, intestine; mo, mouth; poe, posterior oesophagus; prb, proboscis; pst, posterior area of stomach; rec, rectum; rs, radular sac; sgl, salivary gland; st, stomach. (D, after Wu 1965)

[A–C, W.F. Ponder; D, C. Eadie]

short to very long. There is an accessory boring organ on the anterior sole and the anterior gut has a large pair of salivary glands and, usually, a pair of cylindrical to globular accessory salivary glands. The rachiglossate radula consists of multicuspitate central teeth and a single row of simple, sickle-shaped lateral teeth on each side. There is a large, triangular gland of Leiblein and a prominent valve of Leiblein and the stomach is sac-like, with a broad posterior area, but no caecum. The pallial roof has a prominent anal gland and a hypobranchial gland which often produces a secretion that turns purple on exposure to light.

This group was recognised last century by many authors in much the way we have recognised it here, but has more recently been split by many workers into several families and subfamilies. For example the Rapaninae (= Thaidinae or Thaididinae) are treated here as a subfamily of the Muricidae (following Ponder 1973a; Boss 1982; Kool 1987, 1993), but this group is often given family status. A number of subfamilies have been recognised by various authors (for example, Radwin & D’Attilio 1976), but there appears to be intergradation between the groups (see Ponder 1972b; Kool 1993). We have not used subfamilial groups because of their continuing confused status, but a listing of available names can be found in the work of Ponder & Warén (1988) who recognise only the Muricinae, Thaidinae (= Rapaninae following Kool 1993) and Coralliophilinae. They are usually accorded full family status, but are considered to differ in only minor ways (notably the loss of the radula) from other muricids. However, recent anatomical work by Kantor (1995) suggests that this group is sufficiently discrete from muricids to be recognised as a separate, perhaps somewhat convergent, family. Subfamily names used by Wilson (1994) are: Coralliophilinae, Ergalataxinae, Muricinae, Muricopsinae, Thaidinae (now Rapaninae), Trophoninae and Typinae. Kool (1993) recognised Rapaninae (= Thaidinae) and Ocenebrinae (= Ecphorinae, Nucellinae), the former group accommodating genera such as *Dicathais*, *Cronia*, *Drupa*, *Morula* and *Thais*; the latter, *Haustrum* (possibly including *Lepsiella*) as well as *Nucella* and other extralimital genera. The Muricidae are popular with shell collectors and several semipopular reviews have been published (Smith, M. 1953; Fair 1976; Radwin & D’Attilio 1976; Kosuge & Suzuki 1985). Australian muricids have been treated in some detail by Wilson (1994).

Shells range in size from 6 to over 300 mm in length, and are variable in shape (Fig. 15.156) – from limpet-like to spindle-shaped – and in ornamentation. The protoconch varies from paucispiral to multispiral and may be smooth or ornamented. Species with planktotrophic larvae have a multi-whorled protoconch. The shell surface may be smooth, but is usually elaborately spirally and axially ribbed. An intritacalx is sometimes present. The sculpture is often scabrous to lamellate and often there are prominent varices that bear spines or, in some species nodules; the Typhinae, often treated as a subfamily or even as a family, have long tubular spines. The aperture often has denticulations on the inner surface of the labial lip, but the columella is usually simple. The siphonal canal ranges from short to very long, and can be open or closed. The posterior sinus is usually indistinct, but is drawn into a tube in the Typhinae. The horny operculum is thin to thick and has a terminal or lateral nucleus.

The cephalic tentacles are short to elongate, have the eyes on their outer sides, and elongate bases. The foot is truncate anteriorly and typically has an accessory boring organ on the antero-ventral surface, the fine structure of which is described by Nylen, Provenza & Carriker (1969).

The ctenidium is well developed, the osphradium is large and bipectinate and the hypobranchial gland is very well developed and in some species produces a purple secretion. The kidney is of the pycnonéphridien type with the primary and secondary lamellae interdigitated. The circumoesophageal ganglia are concentrated as a nerve collar behind the valve of Leiblein. The cerebral and pedal commissures are short and each statocyst has a large statolith.

The central radular teeth (Fig. 15.157A–C) usually have three primary cusps and, in many genera, intermediate, smaller cusps or denticulations. The simple lateral teeth have broad bases and the single cusp is recurved and pointed. The alimentary canal (Fig. 15.157D) has a proboscis that is usually short, a pair of salivary glands and accessory salivary glands, a large valve of Leiblein, and a gland of Leiblein and a large anal gland (Wu 1965; Ponder 1973a; Harasewych 1984; Kool 1993).

Radwin & D'Attilio (1976) listed four feeding techniques. Usually a hole is bored in the shell of the prey with alternate use of the radula and the accessory boring organ (Carriker 1961; Nylen *et al.* 1969). An uncommon technique involves pulling apart the shell of the prey species with the foot (Wells, H.W. 1958). A third technique is where the muricid grips the bivalve shell tightly with the foot, delivers blows to the lip margin of the bivalve with its outer apertural lip to open a small crack and then inserts the proboscis between the valves. The fourth method of feeding involves use of the long, sharp pegs (labial spine) on the outer lip to pry open the shell valves and insertion of the proboscis. Some species are highly prey specific, but many are generalist feeders (Radwin & D'Attilio 1976; Taylor, J.D. 1976, 1977), eating a wide range of prey including barnacles, limpets, vermetid gastropods, oysters (Pl. 27.5), mussels, sipunculids, polychaetes and small crustaceans. For example, Wu (1965) recorded species of *Drupa* feeding on holothurians and bivalves, as well as carrion, and J.D. Taylor (1983) and Thomas & Kohn (1990) reviewed the diets of *Drupa* species and showed that they feed mainly on polychaetes, crustaceans and vermetid gastropods. Species of *Drupella* feed on scleractinian corals (Taylor, J.D. 1976; Moyer, Emerson & Ross 1982). Coralliophilines, all of which lack a radula, also feed on corals, some such as *Coralliophila* living on them externally, and others such as *Magilus* and *Leptoconchus* living internally in hard or soft corals. There is little data on what coralliophilines are actually eating. They probably feed directly on the coral polyps, but studies on their biology are few (Ward 1965; Brawley & Adey 1982; Haynes 1990).

Sexes are separate, but imposex has been recorded in a number of species (see Fioroni, Oehlmann & Stroben 1991 for review). The male has a dorso-ventrally flattened penis. Females typically have an ingesting gland, a gono-pericardial duct and a small bursa copulatrix. A seminal receptacle is sometimes present and the glandular part of the oviduct consists of a posterior albumen gland and an anterior capsule gland. Protandrous sex change has been demonstrated in *Coralliophila violacea* (Soong & Chen 1991). Duration of copulation varies from species to species, from a few minutes to several days (intermittently) (Radwin & D'Attilio 1976). Females sometimes will mate more than once. Eggs are deposited in fibrous egg capsules (D'Asaro 1991), usually in clusters, and sometimes united by a basal membrane, on a firm substratum. Several animals may lay their egg capsules together, forming large communal egg masses. Some capsules are lens shaped (for example, those of *Cronia*, Phillips 1975), others have pedunculate bases and some are laid in vase-shaped masses. The shape of the capsule is determined in part by the shape of the special pedal gland in the anterior foot which is used to mould the capsules (Radwin & D'Attilio 1976). Variable numbers of eggs are encased in each capsule and sometimes eggs act as nourishment for developing embryos (Radwin & D'Attilio 1976). Generally each capsule has one or more emergence hatches (opercula) apically (Hancock 1956). The duration of embryonic and larval development varies considerably between species, and ecological factors can influence development within a species (Radwin & D'Attilio 1976). Larval development may be direct or indirect. In some genera there are species that are indirect developers with a swimming veliger larva (see Fig. 14.35) and others that are direct developers. Brooding behaviour is reported in some American species of *Phyllonotus* and in one species, *P. regius*, the female remains on or near the communal egg masses for several weeks. Coralliophilines hold the egg capsules in the pallial cavity (see Fig. 14.33; Gohar & Soliman 1963; Wells, F.E. & Lalli 1977).

The family Muricidae is cosmopolitan, living mainly in shallow tropical and subtropical waters, typically inhabiting rocky areas, although some species live on soft substrata (for example, *Murex* species; Pl. 27.4). Some species have very specific habitats, an example being the American *Urosalpinx cinerea*, an oyster predator, that can be controlled by having a soft, muddy bottom free of rocks around the oyster bed because this species avoids crossing soft substrata (Carriker 1955). The relatively large size and abundance of muricids make them ideal subjects for ecological studies (for example, Phillips 1969; Phillips & Campbell 1974; Bayliss 1982; Moran, Fairweather & Underwood 1984; Fairweather 1988; Tong 1988 – this being a very small sample of the literature).

Tyrian purple (purple hypobranchial secretion) was obtained, historically, by crushing shells of *Bolinus brandaris* and *Hexaplex trunculus*, and was used to colour robes, parchments and other articles for royal use. This secretion is reported to be toxic (Clench 1947); it contains mercaptans and choline esters which are toxic to crabs and fish, but harmless to mammals. Roller, Rickett & Stickler (1995) gave a detailed description of the structure and function of the hypobranchial gland of an American species, *Stramonita haemastoma canaliculata*; the function of the secretion is still uncertain. *Concholepas peruviana*, a limpet-like species related to *Thais*, is harvested commercially in western South America and some species of *Thais* and its relatives are also eaten. Several species are serious pests on oyster and mussel beds, and *Drupella* has been identified as a serious cause of coral damage on reefs in northern Western Australia and elsewhere in the Indo-West Pacific (see references in Johnson & Cumming 1995).

There are numerous nominal genera in this family, but their limits are often ill-defined and there is considerable dissension about the status of many genera. Many of the species found in Australia have an Indo-West Pacific distribution, but others are restricted to Australian waters. Wilson (1994) gave a detailed review of the Australian fauna which is too large to list here apart from a brief mention of a few particularly notable genera. *Chicoreus* with shells characterised by having three more or less foliaceous varices (Fig. 15.156B), is represented by at least 16 Australian species (Houart 1992). *Murex* species have spindle- or club-shaped shells (Fig. 15.156A) and three varices per whorl, each bearing short to long, simple, partially or entirely closed spines; there are at least nine Australian species (Ponder & Vokes 1988). The morphologically similar *Haustellum* has a long siphonal canal like *Murex* and has several species in Australia. There are several Australian species of *Typhis* and related genera having a shell with varices, and with tubular spines on or between the varices (Fig. 15.156H). Some genera have a calcified periostracum, including *Aspella* with three Australian species and *Dermomurex* (see Vokes 1985). *Drupella* has a shell very similar to those of *Morula* (Fig. 15.156E) and *Cronia*, but has a distinctive radula with very elongate lateral teeth. *Morula* shells are generally biconic and sculptured with a variable number of rows of nodules and striae, and there are at least seven Australian species. *Drupa* (Fig. 15.156F) differs from *Morula* in having a more sub-ovate form, lower spire, longer aperture and a structurally different central tooth and is represented in Australia by at least six species (Emerson & Cernohorsky 1973). *Pterynotus* has trivariate shells with more or less expanded varical flanges. There are four named species in the subgenus, or closely related genus, *Pterochelus* in Australia (Vokes 1993). The only species truly referable to *Lepsiella* is the common temperate Australian species *L. vinosa*. This genus, possibly synonymous with *Haustellum*, is one of several trans-Tasman links with the New Zealand fauna. Another is the species, *Dicathais orbita*, the large, common cartrut whelk (Fig. 15.156D) found in temperate Australia and also in New Zealand. Both countries also have rich faunas of small-sized taxa related to *Trophon* and *Trophonopsis* (the so-called Trophoninae). These taxa are poorly known and many are found only on the continental slope. Vokes (1974) noted some close similarities between American fossil taxa and Australian species. *Bedeva* (Fig. 15.156C) is represented by two species that have small, fusiform, high-spired, nonvaricate shells. *Coralliophila* and

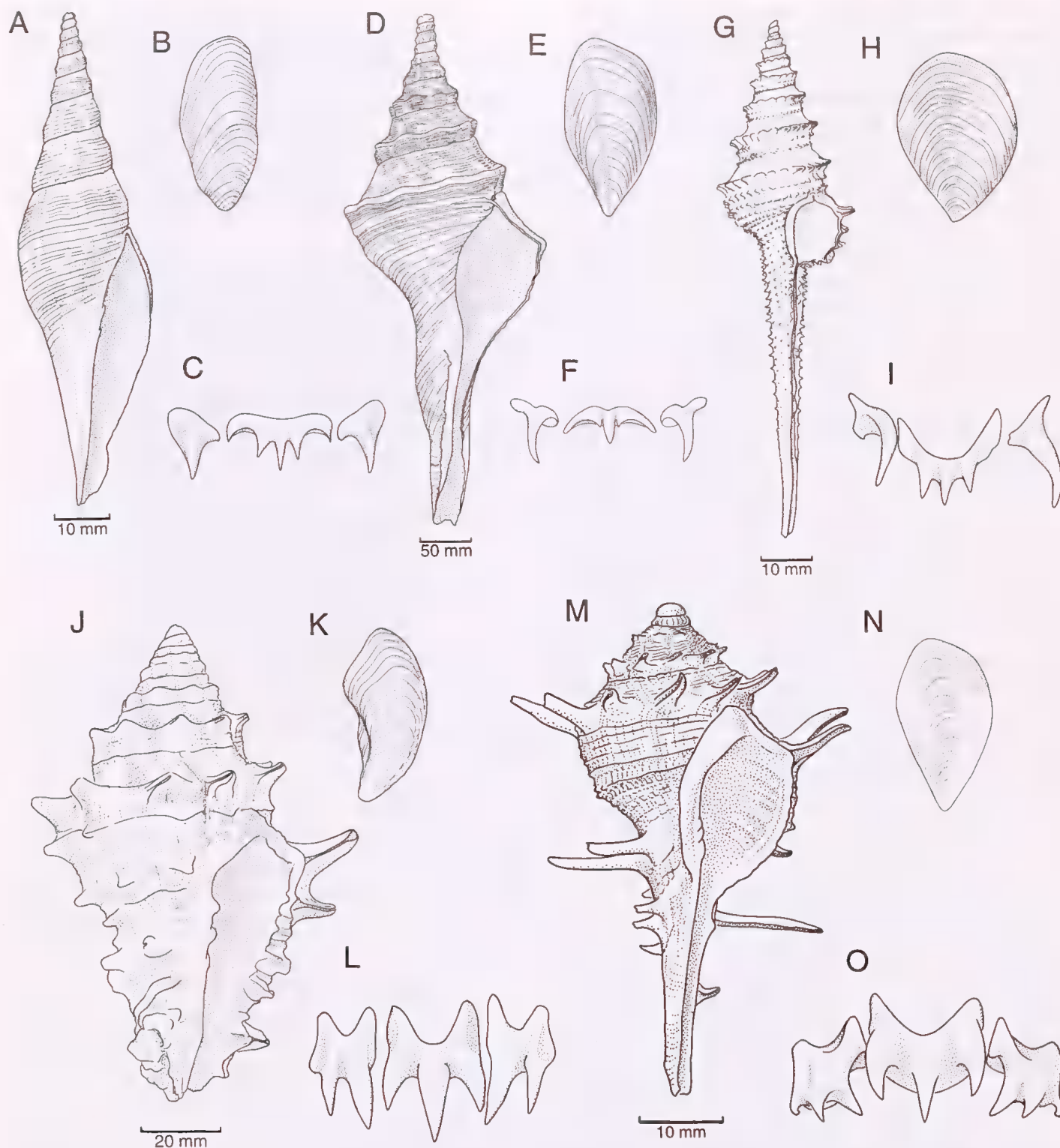


Figure 15.158 Family Turbinellidae. A–C, subfamily Ptychatractinae, *Benthovoluta claydoni*, from the continental slope (350–600 m) off northern Western Australia. D–F, subfamily Turbinellinae, *Syrinx aruanus*, found in the tropical waters from Western Australia to Queensland, in the intertidal zone to 60 m. G–I, subfamily Columbariinae, *Columbarium harrisae*, lives on the continental slope off Queensland, at depths of 240–280 m. J–O, subfamily Vasinae: J–L, *Vasum ceramicum*, occurs in the intertidal to 10 m, from Queensland to the Northern Territory; M–O, *Tudivasum armigera*, from off Queensland, subtidal to 40 m. A, D, G, J, M, shells, apertural view; B, E, H, K, N, opercula; C, F, I, L, O, single transverse rows of radular teeth. [M. Ryan]

Latiaxis and their allies generally have rather squat shells which are often elaborately sculptured (Fig. 15.156G). These genera and the related *Magilus*, which develops a tube-like shell as it grows inside stony corals (Massin 1982), are all represented in Australia.

The earliest undoubted muricids are of Palaeocene age (species of *Poirieria*, *Paziella* and *Pterynotus*; Vokes 1971), although J.D. Taylor *et al.* (1980) have recognised the family in the Lower Cretaceous (Albian). Muricids have been recorded as far back as the Eocene in Australia. In particular the fossil fauna includes species in the genera *Pterynotus*, *Murex*, *Typhis*, *Thais*, *Lepsiella* and *Dicathais*.

Family Turbinellidae

The marine family Turbinellidae is characterised by having a large (20–1000 mm), heavy (Turbinellinae, Vasinae) to thin (most Columbariinae and Ptychatractinae), fusiform to biconical, strongly to weakly shouldered, aragonitic shell, usually with a long, open, axially orientated siphonal canal, and a columella with zero to four plicae (Fig. 15.158A, D, G, J, M). Axial sculpture ranges from prominent spines to low nodes that may be restricted to the early whorls of some taxa. Spiral sculpture may consist of scales or low broad cords, and is usually restricted to below the shoulder and especially along the proximal portion of the siphonal canal. The

protoconch is large and bulbous with the first whorl deviated by up to 80° , ranges from one and a half to more than five whorls, and may not be completely calcified at its apex. Shell colour is usually uniformly white to tan, although some taxa may have darker, reddish-brown patches arranged in rows. The periostracum, consisting of closely spaced axial lamellae, may be thick or thin, yellowish to dark brown, and is usually abraded away everywhere except near the outer lip. The operculum is corneous with a terminal nucleus (Fig. 15.158B, E, H, K, N) and fills the aperture within a quarter whorl of the outer lip in smaller species, but is greatly reduced, narrowly ovate, and vestigial in adults of some larger taxa (for example, *Turbinella*, *Syrinx*, *Benthovoluta*).

Animals generally have a short, broad foot that tends to be black or, in shallow-water taxa, mottled with black; a well-defined siphon; and long cephalic tentacles with eyes near their outer distal ends. The mantle cavity contains a well-developed bipectinate osphradium, a ctenidium and a hypobranchial gland that does not produce a purple secretion. The kidney has lamellae interdigitated (pycnonéphridien type) in all subfamilies except Vasinæ, in which they are separated (méronephridien type). The proboscis is long and narrow (except Ptychactractinae), and the radula is small with tricuspidate central and mono-, bi-, or tricuspidate lateral teeth. The salivary glands are paired, the valve of Leiblein is small, the gland of Leiblein is large and ascinous to small and flaccid. The anal gland is small to large and accessory salivary glands are absent. Reproductive systems are typical of Muricoidea, with the male reproductive system having an open or partially fused sperm groove.

The Turbinellidae, one of the most ancient of neogastropod families, contains five Recent subfamilies, the Turbinellinae, Vasinæ, Columbariinae, Ptychactractinae and Tudiclinae (Ponder & Warén 1988), most with origins in the Cretaceous. All of these subfamilies have, at some time, been regarded as separate families, and are united under Turbinellidae based on overall conchological, radular, and anatomical similarities rather than clearly defined synapomorphies.

Members of the subfamily Tudiclinae may be recognised by their sub-pyriform, strongly shouldered shells with a low spire, a tall, mammillate protoconch, a long, narrow siphonal canal, and the lack of columellar folds. Tudiclines are well represented in the Upper Cretaceous and Palaeogene fossil deposits of the Americas, Europe and Asia, more rarely in the Middle Miocene to Pliocene fossil record of southern Australia (Tate 1888; Ludbrook 1941). The anatomy and ecology of the single extant species, which is restricted to south-eastern India, is unknown.

Vasines have a heavy, biconic shell (Fig. 15.158J, M) with prominent axial ribs that may bear knobs or spines; two to four columellar folds; a long proboscis; a short siphonal canal; and a radula with bi- or tricuspidate lateral teeth (Fig. 15.158L, O). The two genera (one with two subgenera) and seven species that occur in Australia are reviewed and well illustrated by Wilson (1994). The circumtropical genus *Vasum* (about 15 Recent species) is represented in the shallow reefs of tropical northern Australia by *Vasum turbinellum* and *V. ceramicum*, and on the deeper continental shelf of south-western Australia by *Vasum (Altivasum) flindersi*.

The bathyal subfamily Columbariinae is readily recognised by the long, fusiform, shell which has a bulbous, deflected protoconch of one and a half to two whorls (Palaeogene species may have a more conical protoconch with up to 3.5 whorls), a columella without folds; spines or keel on the shoulder; and pronounced, often imbricated spiral sculpture usually most prominent anterior to the periphery and especially along the proximal portion of the long, narrow, axial siphonal canal (Fig. 15.158G). The very long, thin proboscis is retracted and coiled into a non-evaginable sheath. The radula has tricuspidate central teeth and unicuspidate lateral teeth (Fig. 15.158I). The two Recent Australian genera and nine species, as well as numerous fossil taxa were reviewed by Darragh (1969, 1987) and Harasewych (1986); see Wilson (1994) for discussion and colour photographs of the extant Australian taxa.

Five of the seven extant species of the western Pacific genus *Columbarium* occur along the upper continental slope of eastern Australia (*Columbarium harrisae*, *C. hedleyi*, *C. hystriculum*, *C. pagodoides*, *C. spinicinctum*), and four species of the more diverse and wide-ranging Tethyan genus *Coluzea* are known from similar depths off north-western Australia (*Coluzea aapta*, *C. distephanotis*, *C. icarus*) and Queensland (*C. bimurata*). All these species are endemic to Australia. This group was, until recently, regarded as a separate family (Harasewych 1983).

The bathyal to abyssal subfamily Ptychactractinae occurs globally along continental margins, and is readily distinguished by its elongate, fusiform, weakly sculptured shell (Fig. 15.158A); paucispiral protoconch; columella with zero to four weak folds; rounded shoulder; short, broad proboscis that is not folded within a proboscis sheath; and penial papilla. At present, *Benthovoluta claydoni* from the upper continental slope of north-western Australia, is the only known Australian member of this Indo-West subfamily. Harasewych (1987) reviewed the four Recent species of *Benthovoluta* and discussed the anatomy and fossil record of the genus as well as its relationship to the six other genera currently placed in Ptychactractinae. Ptychactractines inhabit sandy bottoms at bathyal to abyssal depths. The stomach contents of one specimen of *Benthovoluta claydoni* included an amphipod carapace, but lacked polychaete setae (Harasewych 1987). The radula is illustrated in Figure 15.158C.

The small, tropical, Tethyan relict subfamily, Turbinellinae, is characterised by having a large, heavy, biconic, pseudo-umbilicate shell (Fig. 15.158D); a columnar, multi-whorled (greater than three whorls) protoconch; a long, broad siphonal canal; a deep furrow on the anterior portion of the foot; a radula with the three cusps of the central tooth concentrated in the mid-section of a strongly recurved basal plate (Fig. 15.158F); as well as by the lack of a bursa copulatrix (Harasewych 1987). *Syrinx aruanus*, which may reach a metre in length, is endemic to western and northern Australia and Papua New Guinea and is the only turbinelline in Australian waters. The monotypic genus *Syrinx* differs from most members of the subfamily in lacking columellar folds. Details of the anatomy of this species are provided by Kesteven (1904) and reviewed by Harasewych & Petit (1989).

Members of the tropical subfamilies Turbinellinae, Vasinæ and Tudiclinae live in sand or coral rubble, subtidally at inner continental shelf depths. All, but the last, the Tudiclinae, are known to feed on endobenthic animals such as tube-dwelling polychaetes, sipunculans, and gaping bivalves (Abbott, R.N. 1959; Taylor, J.D. 1983). Juveniles may burrow, but adults are epibenthic (Hornell 1951; Abbott, R.N. 1959; Bandel & Wedler 1987). Columbariines dwell on sand and rubble bottoms along the upper continental slope. The only recognisable gut contents of all species studied are spicules of tube-dwelling polychaetes. The presence of long, delicate spines, as well as attached anemones (Harasewych 1986), indicates that at least some species are epibenthic.

Like other neogastropods, turbinellids are all gonochoristic, and fertilisation is internal. Eggs are deposited in leathery capsules. Capsules of *Vasum* are biconvex and deposited singly (Bandel 1976b), whereas those of *Turbinella* and *Syrinx* have a broad keel and are attached to each other, forming strands (Hornell 1951; Bandel 1976b). Development is direct (Hornell 1951; Bandel 1975); the capsules contain nurse cells.

Family Buccinidae

Members of the primarily marine family, Buccinidae, have small to medium-sized (20–250 mm), globose, ovate to fusiform, strongly to weakly shouldered shells with an open siphonal canal or siphonal notch, and usually have a smooth columella lacking plicae (Fig. 15.159A, D, G, J, L). When present, axial sculpture usually consists of broad ribs, and may be limited to early whorls; it is most pronounced along the shoulder, forming knobs in strongly shouldered species. Spiral sculpture of strong to weak cords, often with finer intervening threads, usually occurs. The base colour of shells is usually white to tan and darker spiral

15. PROSOBRANCHS

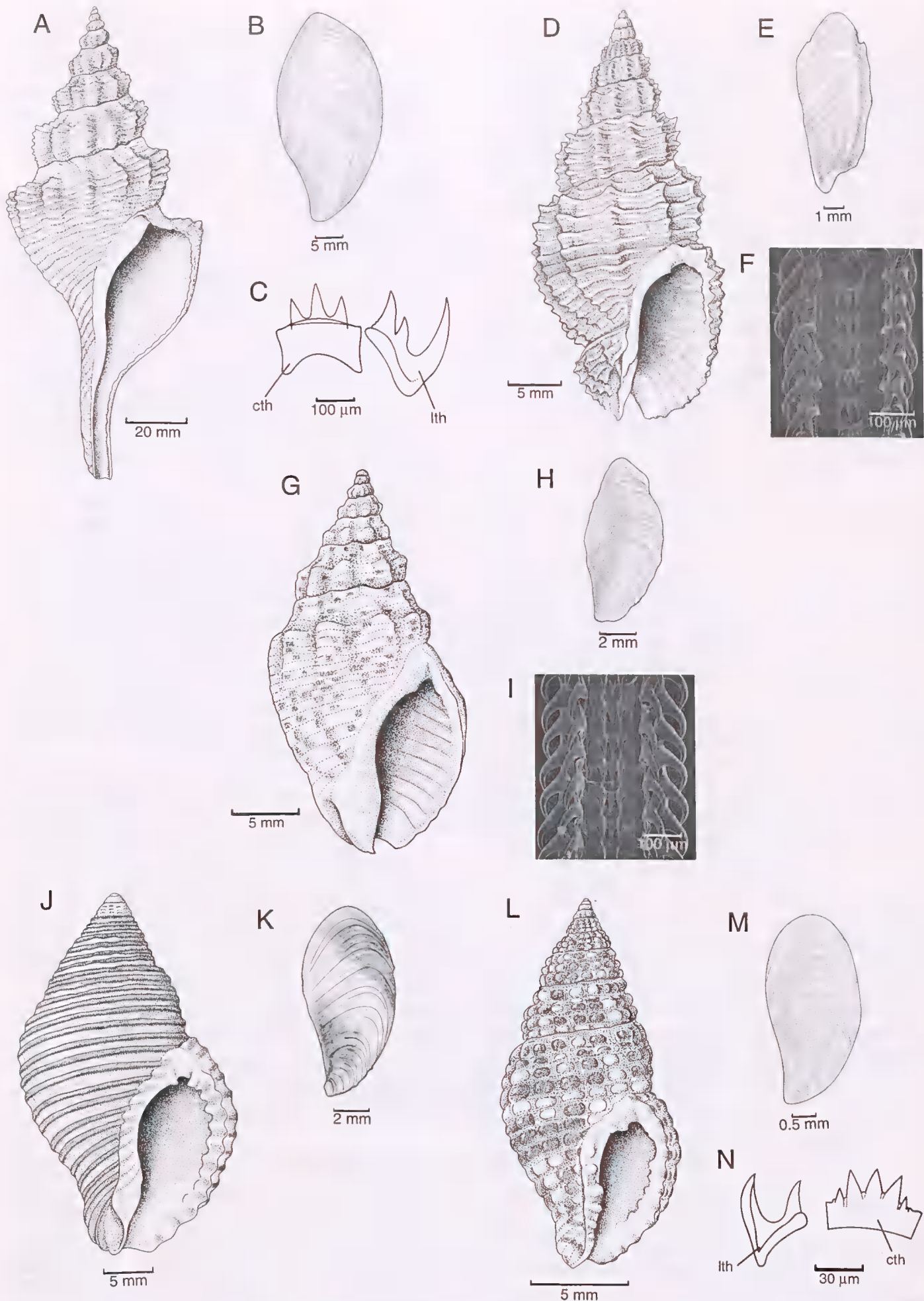


Figure 15.159 Family Buccinidae. A–C, subfamily Buccininae, *Penion mandarinus*. D–I, subfamily Photinae: D–F, *Phos senticosus*; G–I, *Cominella* (*Josepha*) *eburnea*. J–N, subfamily Pisaninae: J, K, *Cantharus undosus*; L–N, *Engina armillata*. A, D, G, J, L, shells, apertural view; B, E, H, K, M, opercula; C, N, central tooth and one lateral tooth of a single transverse row of radular teeth; F, I, several transverse rows of radular teeth. cth, central tooth; lth, lateral tooth. (C, after Ponder 1972c; N, after Ponder 1973a) [A, D, G, J, L, S. Weidland; B, C, E, H, K, M, N, C. Eadie; F, I, M.G. Harasewych]

bands of reddish brown may occur along the shoulder, at mid-whorl, base or tip of the siphonal canal, and/or be confined to spiral cords. The protoconch is usually paucispiral, conical, and often differs in colour from the teleoconch. The periostracum is composed of closely spaced axial blades, may be thin or thick, yellowish to dark brown. The operculum (Fig. 15.159B, E, H, K, M) is thick, elongate, has a subcentral or terminal nucleus (usually abraded), and may fill the aperture in many smaller and tropical species, but is reduced in some larger temperate, polar, and deep-water species. The absence of accessory salivary glands and an anal gland is characteristic of the Buccinidae and of the related 'families' Melongenidae, Fascioliariidae, and Nassariidae (Ponder 1973a). Buccinids are usually distinguished from these 'families' by the presence of a radula with three or more cusps on the central teeth, and lateral teeth with two large flanking cusps and zero to five smaller intermediate cusps (Fig. 15.159C, F, I, N). Descriptions of the anatomy of several shallow-water, primarily boreal taxa have been published (for example, Dakin 1912; Golikov 1980; Kantor 1990b).

The systematics of the Buccinidae are poorly understood, and there is no consensus as to the limits of the family or of the relationships of the more than 200 included genera or subgenera. The family Buccinidae, as presently conceived is probably both para- and polyphyletic. Powell (1951) distinguished the Buccinidae from the Neptuneidae and Buccinulidae on radular and opercular characters, and indicated that the Buccinidae and Neptuneidae are boreal families, whereas the Buccinulidae are restricted largely to the southern oceans. In a review of the New Zealand species of *Buccinulum*, Ponder (1971) noted that anatomical characters are not sufficient to justify even subfamilial separation of buccinulids from the Buccinidae. Habe & Sato (1973) reduced the Neptuneidae to one of the six northern Pacific subfamilies (Buccininae, Neptuneinae, Ancistrolepisinae, Parancistrolepisinae, Liomisusinae and Volutopsiinae) within Buccinidae, but made no reference to the Buccinulidae in their classification. Citing the paucity of differentiating anatomical features, Ponder (1973a) and later Ponder & Warén (1988) included the above taxa within the subfamily Buccininae and reduced Melongenidae, Fascioliariidae, and Nassariidae to subfamilies of Buccinidae. While recognising the close relationship of the Melongenidae, Fascioliariidae and Nassariidae to the Buccinidae, these taxa are provisionally retained as separate families within this volume, and Buccinidae is used in the traditional sense of Thiele (1929–1935), Wenz (1943), and Bouchet & Warén (1985a, 1985b). Vaught (1989) divided the Buccinidae into the subfamilies Buccininae, Volutopsiinae, Photinae, and Pisaninae. Of these, only Volutopsiinae is not represented in Australian waters. Species of *Colubraria* and its relatives have sometimes been placed in their own family, the Colubrariidae. Beu & Maxwell (1987) concluded that they belong in the Buccinidae near *Pisania*, and do not warrant their own subfamily.

The family Buccinidae is represented in the Lower Cretaceous (Albian; Taylor, J.D., Morris & Taylor 1980), ranking among the oldest of neogastropod families. Like most neogastropod families, Buccinidae are thought to have evolved in temperate climatic zones at higher latitudes (Sohl 1987). Although the majority of the neogastropod families became predominantly tropical during the Cainozoic, most Buccinidae remained in temperate and polar regions, where their diversity has increased since the Miocene (Taylor, J.D. *et al.* 1980). Buccinids form a significant component of the neogastropod fauna at bathyal and abyssal depths (Bouchet & Warén 1985a, 1985b).

Although some genera are adapted to hard substrata, most buccinids inhabit subtidal rubble or sand substrata. Diets of some taxa are limited to specific prey items, but the majority of species for which diets have been recorded are more generalised predators or scavengers (Pearce & Thorson 1967; Nielsen 1975; Taylor, J.D. 1978a; Taylor, J.D. *et al.* 1980). Some species of *Cominella* can actively bore holes in the shells of their prey (Peterson & Black 1995).

Buccinids are gonochoristic and fertilisation is internal. Several hundred to several thousand eggs are deposited in leathery capsules that may be stalked and deposited singly, or hemispherical and deposited in clusters. Only a fraction of these develop, as they do so, consuming the remainder which serve as nurse eggs (Portmann 1930; West, D.L. 1973, 1978a, 1978b, 1978c). Larvae may hatch as veligers and undergo a pelagic stage, or may metamorphose prior to hatching and emerge from the egg capsules as crawling young. Detailed descriptions of reproductive biology and development of selected species have been given by Portmann (1930) and D.L. West (1973, 1978a, 1978b, 1978c). Pseudohermaphroditism (imposex) has been reported in some populations, possibly a consequence of pollution (Kantor 1984).

The more widespread tropical buccinid genera such as *Cantharus*, *Engina*, *Pisania* and *Phos* are well represented in Australian waters (Ponder 1972c), and the genus *Penion* (reviewed by Ponder 1973b) is restricted to the temperate regions of Australia and New Zealand. The more common shallow-water species were figured by Wilson & Gillett (1971) and Wilson (1994), and Bouchet & Warén (1985b) illustrated many of the deep-water genera and species, including the endemic *Kapala kengrahama*, *Cominella* (*Josepha*) (which also occurs in New Zealand) and *Fax*.

Family Columbellidae

Columbellids, or dove shells, are small to medium-sized marine snails. Most are operculate and have biconical to elongate-ovate shells with a short anterior canal and narrow aperture, the outer lip often being denticulate and the inner (columellar) lip often plicate. The columbellid radula is typically rachiglossate, but distinctive in having a flat, thin, subrectangular, non-cuspidate central tooth, flanked on each side by a single, sigmoidal, bicuspidate or tricuspidate lateral tooth. Anatomically the family can be distinguished from buccinids by the lack of a stomach caecum, and in males of some species, by presence of a penial pouch.

The first names for columbellids were introduced by Linnaeus (1758) for Mediterranean and Atlantic species. Bruguière (1789) was the first to name an Australian species (*Columbella punctata*, as *Buccinum punctata*), and Lamarck (1799) introduced the generic name *Columbella*. Swainson (1840) established additional genera and raised the group to family level. In his checklist of Australian Recent and Tertiary species, Cotton (1957) listed the Australian collumbellid species, but no other comprehensive cover of Australian collumbellids has been published. Thirteen genera and four subgenera are currently recognised in the Australian fauna, and at least 64 species (Wilson 1994).

Shell form in the family is extremely variable; they range from ovate (*Pyrene*, *Pseudanachis*), ovate-fusiform (*Anachis*, *Zafra*, *Retizafra*, *Mitrella*, *Pseudamycla*) to, more rarely, elongate (*Aesopus*, *Parviterebra* and *Zella*) (Fig. 15.160). With few exceptions the protoconch of columbellids is conical or domed, and consists of one to three whorls; the Australian species *Aesopus pallidulus*, is unusual in having a bulbous protoconch. External teleoconch sculpture when present consists of strong axial ribs (for example, *Anachis*). Spiral sculpture is usually restricted to weak anterior cords, but in some genera (for example, *Galliffena*, *Macrozafra*) there are both axial and spiral ribs producing a strongly reticulate sculpture. In many columbellids, the outer lip is strongly toothed. The teeth are located on a prominent central thickening on the inside of the lip in *Pyrene*. The columella may also be denticulate. In some genera (for example, *Parviterebra*, *Zella*), the outer lip and columella are smooth.

Although no studies have been published on the anatomy, natural history or ecology of any Australian columbellid, we have some knowledge of the biology of these very common animals based on work carried out in other parts of the world (Risbec 1954; Marcus, Er. & Marcus, Ev. 1962; Marcus, Ev. & Marcus, Er. 1964b; Kantor & Medinskaya 1991).

15. PROSOBRANCHS

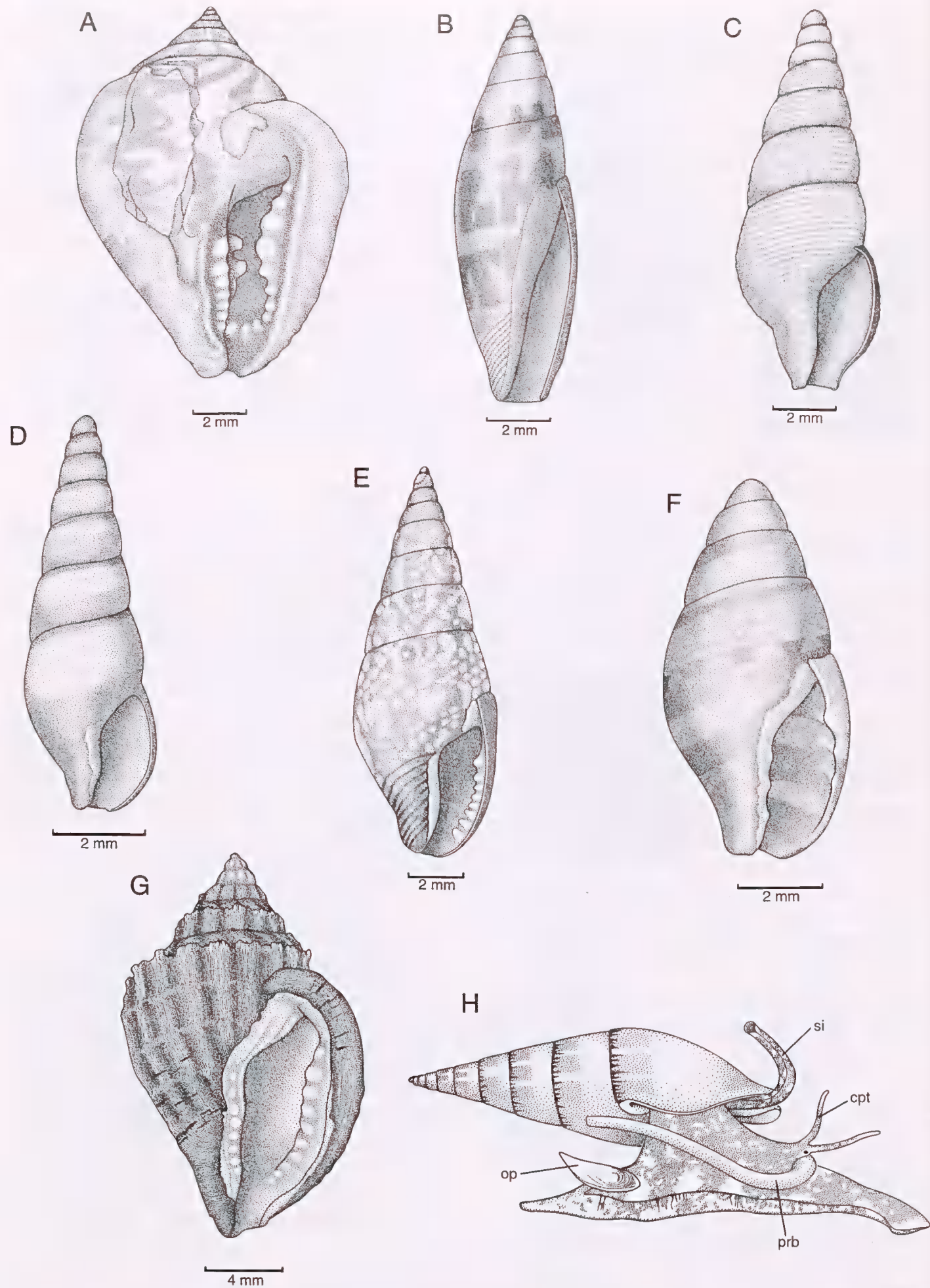


Figure 15.160 Family Columbelloidea. A–G, shells, apertural view: A, subfamily Columbelloinae, *Pyrene turturina*; B–G, subfamily Pyreninae: B, *Parviterebra brazieri*; C, *Aesopus plurisulcatus*; D, *Zella beddomei*; E, *Mitrella lincolnensis*; F, *Pseudamycla dermestoides*; G, *Pseudanachis duclosianus*. H, *Mitrella lincolnensis* crawling with its long proboscis everted. cpt, cephalic tentacle; op, operculum; prb, proboscis; si, siphon. (H, after Wilson 1994)

Externally there is little to distinguish the columbellid animal (Fig. 15.160H) from buccinids. The head is small, without a snout, bearing pointed, divergent tentacles with lateral eyes. The siphon is usually about half the length of the foot. The foot is narrow, truncate at the front, pointed behind, and has a deep, transverse, ciliated, anterior groove into which open the anterior pedal glands. In females there is usually a distinct, pit-like posterior pedal gland appearing as a longitudinal, folded pouch anterior of the mid-point on the sole (Marcus, Er. & Marcus, Ev. 1962; Marcus, Ev. & Marcus, Er. 1964b). An operculum is usually present, but is lacking in some small species (Risbec 1954).

Columbellids are unusual in that they eat both plant and animal material. *Mitrella* and some species of *Anachis* are said to be carnivores. The North Pacific *Mitrella burchardi* feeds predominantly on *Littorina*, crustaceans and polychaetes (Kantor & Medinskaya 1991). The remains of polychaetes, crustaceans and ascidians were found in the stomachs of several species of *Anachis* and *Nitidella* (Marcus, Er. & Marcus, Ev. 1962; Marcus, Ev. & Marcus, Er. 1964b). In contrast, *Columbella mercatoria* is said to be herbivorous (Marcus, Er. & Marcus, Ev. 1962), although it will also take carrion and may be reared in aquaria fed solely on the meat of fish or bivalves (Bandel 1974b; Hatfield 1979). Nielsen & Lethbridge (1989) found diatoms, red algae and the remains of hydrozoans, amphipods and crustaceans in the stomachs of the Western Australian *Pyrene bidentata*, a species which lives epiphytically on seagrasses and appears to be naturally omnivorous.

Details of the musculature and histology of the proboscis, odontophore and the oesophagus have been described (Marcus, Er. & Marcus, Ev. 1962a; Marcus, Ev. & Marcus, Er. 1964b; Kantor & Medinskaya 1991). Columbellids have a long, mobile, pleurembolic proboscis, equipped with numerous, large retractor muscles. It is capable of extension to reach any part of the shell. In the herbivorous *Columbella* species there is a cuticular ring around the opening. The salivary glands are paired; the left gland is smaller than the right, and their ducts open in the posterior part of the buccal tube. Typically, there is a large valve of Leiblein that is cone-shaped and located in front of the nerve ring. The gland of Leiblein is small with a short duct opening into the posterior part of the mid-oesophagus on the right side.

The stomach is large and U-shaped and has no caecum. The anterior part of the stomach is lined with longitudinal folds continuous with the folds of the oesophagus. The central part is lined with low, transverse, cuticularised folds. The major typhlosole is poorly developed. A gastric shield is well developed in the herbivorous *Columbella mercatoria* and *C. rustica* (Marcus, Er. & Marcus, Ev. 1962), but small in *Anachis* and absent in the carnivorous *Mitrella burchardi* (Kantor & Medinskaya 1991). There are two openings from the digestive gland near the centre of the stomach, the anterior one being larger than the other.

The radula is long, and has a tooth formula of 1-1-1 with many rows of teeth. The central tooth is typically rectangular to slightly crescentic, flat and thin and bears no cusps though the posterior corners may be pointed. The central tooth is flanked on each side by a single, sigmoidal, bicuspidate or tricuspidate lateral tooth. The laterals have a basal part lying at right angles to the larger, curved (sickle-shaped), cuspidate upper part. The prong-like cusps may be pointed or blunt. The lateral teeth are movable – they may be turned outward or inward so that right and left cusps touch over the central tooth. The radulae of herbivorous species tend to be broader, with stronger cartilaginous support than the radulae of the carnivorous species. The radulae of *Pseudanachis* (Thiele 1924) and *Pseudamycla* (Pace 1902b) are atypical, having multicuspitate central and lateral teeth; there is some doubt as to whether these genera really belong in this family.

The anatomy of the genital system has several unusual features, especially in the male system. In some Atlantic species of *Anachis*, *Nitidella* and *Columbella* the distal end of the penis, when at rest, lies within a pouch between the hypobranchial gland and the pallial roof (Marcus, Er. & Marcus, Ev. 1962; Marcus, Ev. & Marcus, Er.

1964b; Houston 1976; Houston & Hatfield 1981). However, this is not a universal feature, as in other species the resting penis is merely bent and lies free within the mantle cavity. In some of the species studied, males have a seminal vesicle but no prostate gland, whereas in others there is a prostate, but no seminal vesicle.

Females lay their eggs in flask-shaped or hemispherical capsules, deposited in clusters on hard substrata or on algae (see Bandel 1974b). Species of the Atlantic genus *Strombina* lay their dome-shaped capsules in a compact mass on the shells of adults (Cipriani & Penchaszadeh 1993). The spawn of some Indo-West Pacific columbellids have been described by Petit & Risbec (1929), Thorson (1940) and Amio (1963). In most columbellid species the larvae hatch as planktonic veligers, but in some the hatchlings emerge as crawling snails. In a few taxa, the developing embryos feed on nurse eggs within the capsules. J.B. Taylor (1975) found that there are two types of planktonic protoconchs among the Hawaiian columbellids. In some, the protoconch is ribbed and in others it is smooth. Veligers with ribbed protoconchs have four to five velar lobes, and those with smooth protoconchs have two to four velar lobes.

Columbellids live in a range of habitats. The majority of Australian species probably live on hard substrata, either crawling on the underside of stones or on algae that are attached to rocky substrata. *Pyrene bidentata* lives on the fronds of seagrasses and on macrophytic algae on rocky substrata. Some species assigned to *Mitrella* are hard substratum-dwellers, for example, the southern Australian *M. semiconvexa*. Others are sand burrowers, such as the northern *M. essingtonensis* which lives on intertidal sand flats. *Mitrella ligula* and *M. puella* are two tropical species that live in sand associated with coral reefs.

Kantor & Medinskaya (1991) described the feeding behaviour of *Mitrella burchardi*. When feeding on a littorinid, the columbellid turned over the snail and covered the aperture with its foot, but the method of extracting the prey was not observed. In tide pools, this columbellid was observed to travel more than a metre to reach baits of crushed mussel or sea-urchin; then the radula was extended and used to tear strips of flesh from the bait.

Australian columbellids exhibit distribution patterns typical of other marine groups. Most of the genera (for example, *Columbella*, *Zafra*, *Mitrella*, *Aesopus*) are cosmopolitan or widespread in the Indo-West Pacific Region. Three genera, *Gatliffena*, *Pseudamycla* and *Zella*, are apparently endemic to southern and eastern Australia. *Dentimitrella* is also a southern endemic group, and is here regarded as a subgenus of the cosmopolitan genus *Mitrella*. Most of the northern Australian species are widespread in the Indo-West Pacific region, with little regional endemism. All of the temperate, southern Australian species are endemic to the region.

Family Nassariidae

Species of the marine family Nassariidae are characterised by having a small (4–75 mm), high-spired, ovate to fusiform, strongly to indistinctly shouldered shell with a dorsally reflected siphonal notch (Fig. 15.161A–C). The shell surface may be smooth, or have axial and/or spiral sculpture. Axial sculpture usually consists of broad to narrow, well-defined ribs that may be confined to the posterior portions of the whorls, or may be intersected by spiral threads or cords of comparable width, producing a cancellate to papillose surface. Protoconchs may be multispiral to paucispiral, smooth to carinate, their morphology correlated to the mode of larval development (Cernohorsky 1984); some nassariids have axial costae on the last whorl of the protoconch. The shell aperture is strongly to weakly ovate, the outer lip is usually thickened and frequently forms a varix, denticulate within, with short spines along the anterior edge in some species. The columella is short and twisted, and is smooth or denticulate, with a pronounced siphonal fold. The 'parietal denticle', regarded as diagnostic for the family (Nuttall & Cooper 1973), delimits the adaxial portion of the exhalant channel. The parietal callus ranges from thin and narrow to thick and broad, and

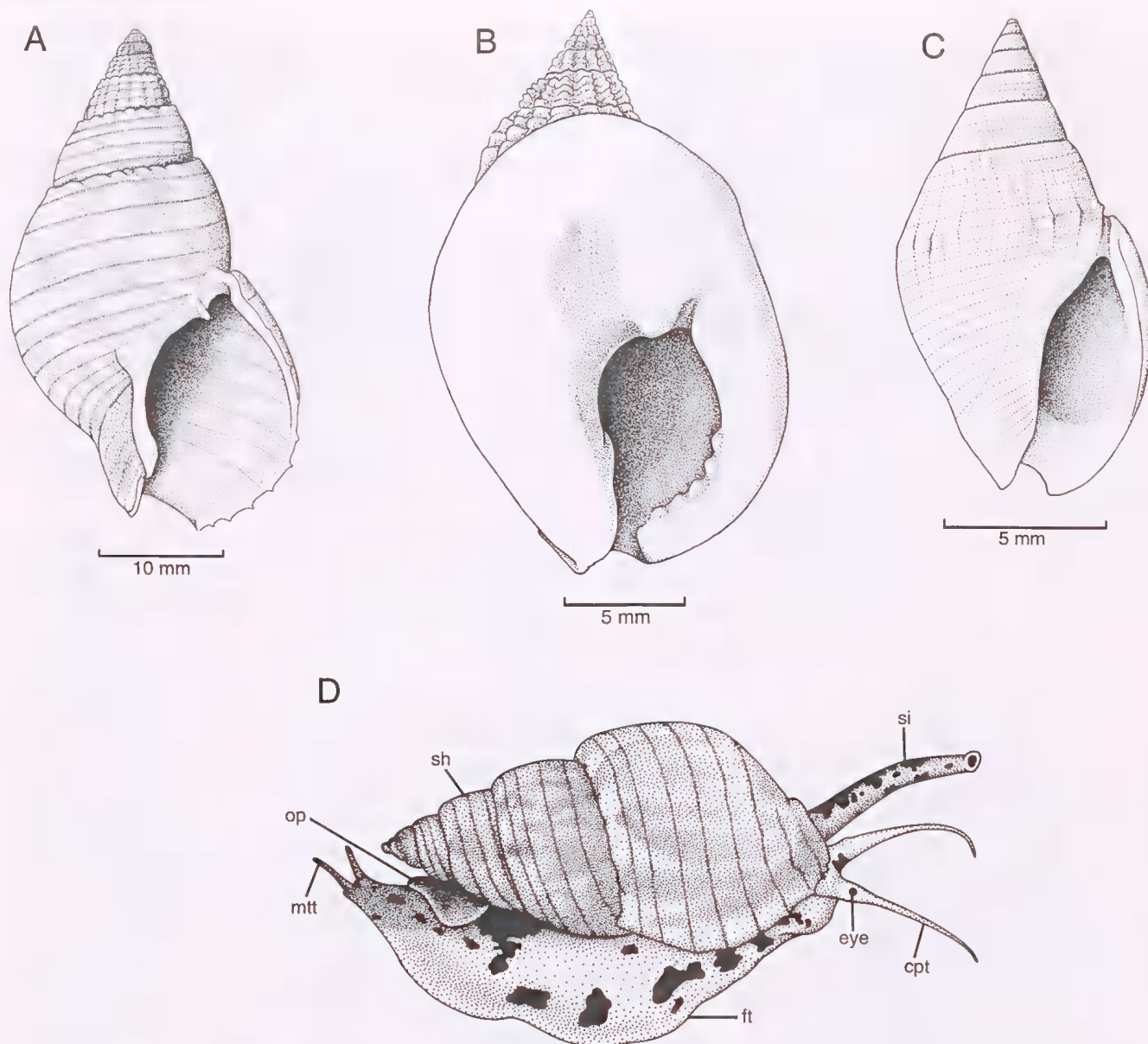


Figure 15.161 Family Nassariidae. A, B, subfamily Nassariinae, apertural view of shells: A, *Nassarius (Alectrion) glans*, lives in waters from the intertidal to 100 m, in northern Australia from Western Australia to eastern Queensland; B, *Nassarius (Plicarcularia) pullus*, found in eastern Queensland. C, subfamily Cylleninae, *Cyllene lactea*, apertural view of shell, endemic to New South Wales, at depths from 7–49 m. D, *Nassarius particeps*, animal, lateral view showing siphon and paired metapodial tentacles. cpt, cephalic tentacle; eye, eye; ft, foot; mtt, metapodial tentacle; op, operculum; sh, shell; si, siphon. (D, after Wilson & Gillett 1971)

[A–C, S. Weidland; D, C. Eadie]

may form a parietal shield extending to the apex in some species. The base colour of the shell ranges from white through tan to dark brown. Darker spiral bands of reddish brown (usually evenly spaced) may occur in lighter coloured species (Pl. 27.6). Dark brown shells may have a band of white at mid-whorl and near the suture. The periostracum is yellow to dark brown and consists of closely spaced axial lamellae, usually abraded away. The operculum is thin and corneous with a terminal nucleus, is reduced in size, and often has serrated lateral margins.

As in Buccinidae, Melongenidae and Fascioliariidae, the anal gland and accessory salivary glands are absent (Ponder 1973a). Most closely related to Buccinidae, the Nassariidae are usually distinguished from buccinids on the basis of their radula having multicuspidate (8 to 19) central teeth, lateral teeth with two large cusps, and accessory plates situated along the inner margins of lateral teeth; a foot that bears two metapodial tentacles on the posterior margin (Fig. 15.161D); an operculum with serrated margins; and a parietal denticle delimiting the exhalant channel.

The division of Nassariidae into three subfamilies, the Nassariinae, Dorsaninae and Cylleninae, has been followed by most authors (for example, Cossmann 1901; Cernohorsky 1981, 1984; Vaught 1989). In addition to having the diagnostic characters listed above for the

family, members of the cosmopolitan subfamily Nassariinae, which contains about 80% of the species in the family (Cernohorsky 1984), may be distinguished by their pronounced shell sculpture (Fig. 15.161A, B), the presence of eyes, and the lack of a sutural groove. The Cylleninae differ from Nassariinae in having a proportionally larger, more elongated aperture (Fig. 15.161C); a prominently lirate and callused columella; a sutural groove; and lateral teeth with long outer cusps and greatly reduced inner cusps. Although present in the fossil record of western Africa, Europe, and Asia, extant members of this subfamily are restricted to western Africa and the Indo-West Pacific. The Dorsaninae may be recognised by their thin, elongate, inflated shells lacking prominent spiral sculpture and in having a radula that lacks accessory plates and has lateral teeth with more than two cusps. This subfamily is represented in the Tertiary deposits of North America and Europe, but in the Recent fauna is restricted to eastern South America, southern Africa and the western Indian Ocean. Following a cladistic analysis of the family, Allmon (1990) removed several genera previously included in Dorsaninae to form the subfamily Bulliinae, which is distinguished from Dorsaninae by lack of a well-developed recurved siphonal canal, the presence of a sharp carina along the fasciole, and by reduced internal and external sculpture.

Nassariids occur primarily in estuarine to shallow marine soft substrata, usually in tropical and temperate regions, and attain their greatest diversity in the tropical Indo-Pacific. Many species are colonial, sometimes occurring in high densities (5000 individuals/m²) (Brown, S.C. 1969). Due to their abundance, nassariids, particularly temperate Atlantic species, have been well studied in terms of anatomy, ecology, developmental biology, and physiology (see extensive bibliographies in Brown, A.C. 1982; Cernohorsky 1984; Allmon 1990). Although most are carnivores feeding on carrion, at least some species can become facultative herbivores, developing a crystalline style in the stomach during such periods (Morton, J.E. 1960; Brown, S.C. 1969). Nassariids are rapid burrowers and some species of Dorsaninae are capable of swimming ('surfing') for short distances by exposing their expanded foot to the surf (Brown, A.C. 1982).

Sexes are separate and fertilisation is internal. Egg capsule morphology varies from simple, lens-shaped oothecae attached directly to hard substrata, to vase-shaped capsules, with stalks varying in degree of constriction (see Cernohorsky 1984, figs 46–75 for overview; D'Asaro 1993). Individual capsules may contain from one to more than 2500 ova. Development may be planktonic (days to months in plankton), ovoviviparous within the pallial oviduct (Kaicher 1972; Cather 1973), or direct (with or without nurse eggs), with egg capsules attached to hard substrata or carried in a tubular brood pouch in the foot (da Silva & Brown 1985). Jenner (1979) reported environmentally mediated pseudo-hermaphroditism (imposex) in some populations.

Nassariidae are the youngest of the families usually included in 'Buccinacea', with species attributed to the subfamily Dorsaninae dating from the Palaeocene, whereas the Cylleninae and Nassariinae first appear in the Miocene.

Cernohorsky (1981) revised the Nassariidae of Australia, recognising 13 Recent and eight Tertiary species. Wilson & Gillett (1971) illustrated in colour 12 of the more common extant species. Wilson (1994) discussed and illustrated 74 nassariid species living in Australia, of which 13 are endemic.

Family Melongenidae

Members of the shallow-water marine family Melongenidae are characterised by having a medium-sized to large (30–400 mm), pyriform to fusiform, strongly-shouldered, pseudo-umbilicate shell with a short, broad siphonal canal and a columella lacking plicae (Fig. 15.162A). Axial folds, when present, are most pronounced on early whorls and on posterior portions of whorls, producing knobs or spines along the shoulder. Spiral sculpture, consisting of weak cords, is most pronounced along the siphonal canal. A raised ridge or an additional row of knobs or spines occurs at the juncture of the last whorl and siphonal canal in some species. Shells range from cream-yellow to dark brown, and may be uniform in colour or spirally banded along the mid-whorl. The protoconch is conical and dark brown. The periostracum is thick and dark brown. The operculum is thick, has a terminal nucleus, and fills the aperture a quarter of a whorl behind the outer lip (Fig. 15.162B, C). In general appearance and anatomical organisation the Melongenidae are similar to the Buccinidae and Fascioliariidae. The long narrow head with short tentacles and distal rhynchostome (aperture through which the proboscis is protruded) are unique to the family (Fig. 15.162D, E). Other diagnostic anatomical features include a jet black to mottled dorsal surface on the foot, an extremely long and narrow proboscis, which is wound into the large proboscis sac when retracted, the mouth situated on the ventral surface of the proboscis just behind the tapered distal end (Fig. 15.162E), a radula with tricuspidate central teeth and bicuspidate lateral teeth (Fig. 15.162F), and a flaccid, ribbon-like gland of Leiblein. The gonads of most caenogastropods line the columellar side of the digestive gland, but melongenines are unusual in having them situated at the apical portion of the visceral mass (that is behind rather than along the digestive gland).

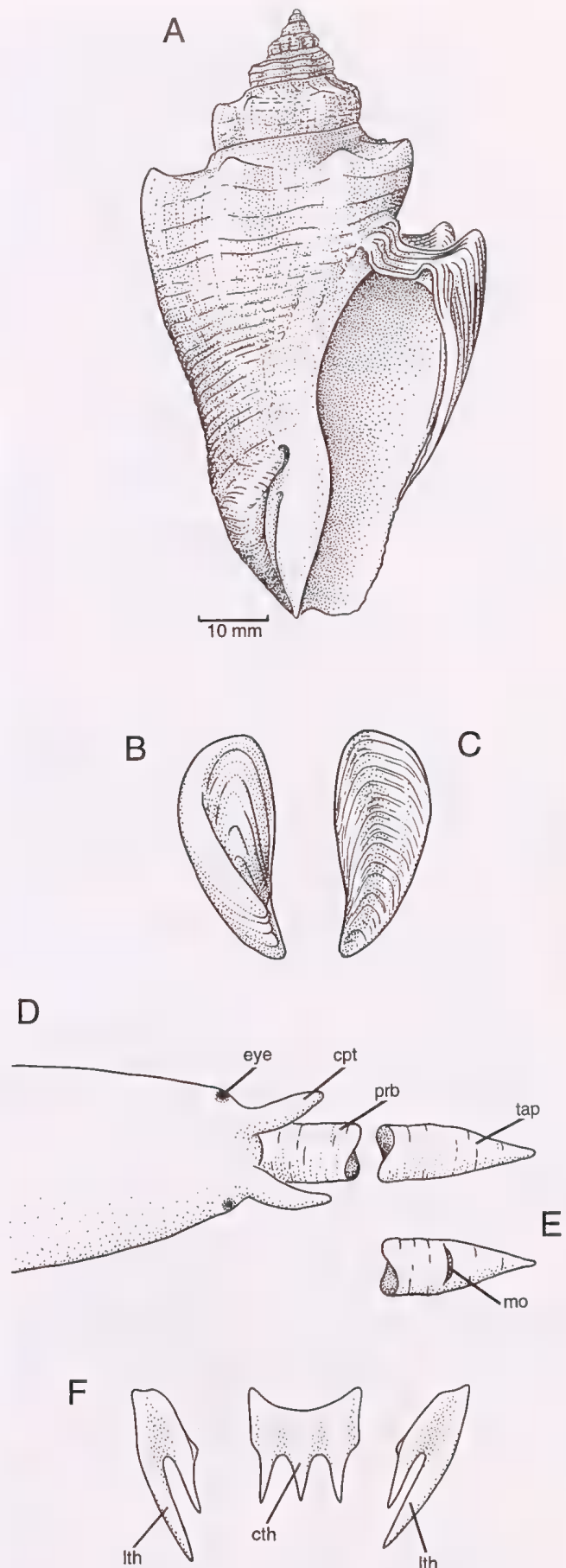


Figure 15.162 Family Melongenidae. *Pugilina cochlidium*, the sole Australian melongenid. A, shell, apertural view. B, C, operculum: B, inner view; C, outer view. D, long narrow head, with the proboscis extended showing the tapering distal end (the mid-section of the proboscis has been removed). E, proboscis tip, ventral view, showing the position of the mouth. F, a single row of radular teeth, showing the bicuspidate lateral teeth and a tricuspidate central tooth. cpt, cephalic tentacle; cth, central tooth; eye, eye; lth, lateral tooth; mo, mouth situated near distal end of long proboscis; prb, proboscis; tap, tapered distal end of the proboscis. [M. Ryan]

15. PROSOBRANCHS

The family is divided into two subfamilies, the Melongeninae, which have a global, primarily tropical distribution, and the Busyconinae, which have always been restricted to the temperate waters of the north-western Atlantic Ocean. The Melongeninae conform in all respects with the family features. Busyconines are readily distinguished by their broader, lower-spined shells with a deflected protoconch and by having a short, broad proboscis, a large buccal mass that fills the cephalic haemocoel, and intermediate cusps on the lateral teeth of the radula; they are not dealt with here in detail.

The Melongenidae are among the oldest of neogastropod families, with the earliest records dating to the Lower Cretaceous (Taylor, J.D. *et al.* 1980). Diversity was greatest during the Upper Cretaceous, and has been declining since. Many of the approximately two dozen Recent species were known to pre-Linnaean authors, and most were described during the second half of the 18th Century (Bayer 1952). Subsequent authors described several deeper water species as well as a large number of subspecies and forms. Hollister (1958) reviewed the two Recent busyconine genera (with five subgenera). Recent species of Melongeninae are referred to the genera *Melongenella* (restricted to the New World tropics), *Volema*, *Hemifusus* (both Indo-West Pacific), and *Pugilina*, which contains one amphiatlantic species and one Indian Ocean species. The genus *Taphon* from the 'China Seas' has been assigned to the Melongenidae by some authors (Wenz 1943; Vaught 1989), however, its true affinities are uncertain.

Melogenids inhabit near-shore sand and mud bottoms, with some taxa prevalent in estuaries and bays, and others on offshore sand bars. Although generally regarded as scavengers, studies have shown that some species prey exclusively on living bivalves (Morton, B. 1985), and others consume carrion in addition to living bivalve and gastropod prey (Hathaway & Woodburn 1961). Where they occur, melongenids tend to be common, with several animals often feeding together on larger prey items (Hathaway & Woodburn 1961).

Melongenids are gonochoristic. Males tend to be smaller and to mature earlier than females (Kumar, Rani, Leela & Ayyakkannu 1988). Fertilisation is internal, and eggs are deposited in leathery biconvex capsules (20 to 150 eggs per capsule). Individual strands, laid by a single female, may consist of six to 150 capsules (Hathaway & Woodburn 1961; Morton, B. 1986a). The entire strand is attached to a hard substratum in the Melongeninae, whereas busyconines anchor one end of the strand below the surface of the sand, the remainder floating above the anchor. Metamorphosis occurs within the capsule, with crawling juveniles emerging at hatching, 20 to 90 days after oviposition depending on the species (Hathaway & Woodburn 1961; Morton, B. 1986a).

The family Melongenidae is represented in Australian waters by a single species *Pugilina cochlidium*, which inhabits intertidal mud flats from the Timor Sea to Torres Strait. Iredale (1938) proposed a new genus (*Volegalea*) and a new species (*wardiana*) for this taxon. *Syrinx aruanus*, the largest living gastropod, had been assigned to the Melongenidae by most authors (Thiele 1929–1935; Wenz 1943), but more recently has been transferred to the family Turbinellidae (Harasewych & Petit 1989). Several melongenine taxa are represented in the Tertiary deposits of Indonesia, but the family has no fossil record in Australia.

Family Fasciolariidae

The marine family Fasciolariidae is distinguished by its medium-sized to large (generally 50–600 mm), strongly to weakly fusiform, high-spined, strongly to inconspicuously shouldered shell, with a well-developed, axial or near axial siphonal canal (Fig. 15.163A, C, D). The aperture is ovate to hemi-elliptical, and the outer lip may be smooth or bear numerous fine spiral lirae. The columella has a pronounced siphonal fold (less prominent in species with a long, siphonal canal) and zero to four columellar plicae. Axial sculpture is present in most taxa and consists of

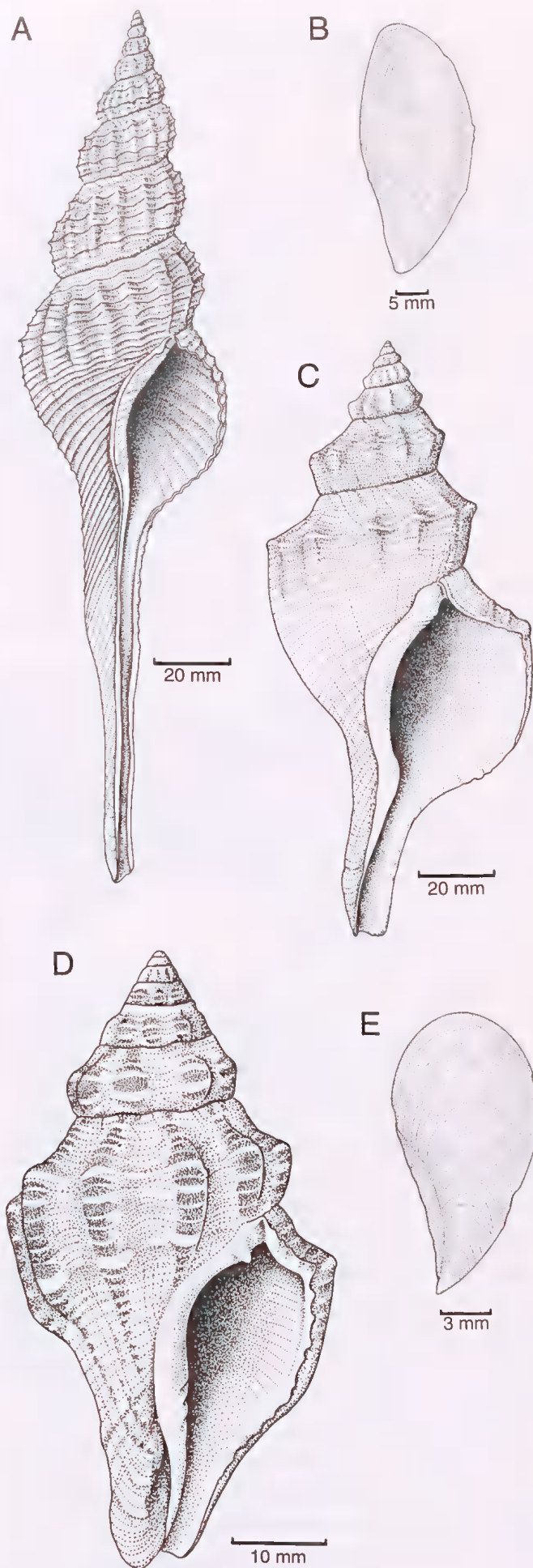


Figure 15.163 Family Fasciolariidae. A, B, subfamily Fusininae, *Fusinus novaehollandiae*; C, subfamily Fasciolariinae, *Pleuroploca australasia*; D, E, subfamily Peristerniinae, *Latirus polgyonius*. A, C, D, shells, apertural view; B, E, opercula. [A, C, D, S. Weidland; B, E, C. Eadie]

broad ribs, most pronounced along and anterior to the shoulder where knobs form in strongly shouldered species. Spiral sculpture may be lacking, but is usually of strong to weak cords that overlie the axial sculptural elements. The basic colour of the shells is usually white, tan, or reddish brown; irregular and/or interrupted axial bands of dark brown may occur along or between the axial ribs, and dark brown spiral bands may occur on or between the prominent spiral cords. The protoconch is paucispiral to multispiral (one and a half to four whorls), conical, often with simple axial sculpture on the last whorl. The well-developed periostracum consists of closely spaced axial lamellae, and is usually thick and yellowish to dark brown; rarely brightly coloured as in *Latirus spiceri* (Pl. 28.3). The corneous operculum is thick and elongate, with a terminal nucleus (Fig. 15.163B, E). The pointed anterior end of the operculum is free of the foot and may be used as a claw (Wells, F.E. 1970).

The Fascioliariidae, like the related Buccinidae, Nassariidae and Melongenidae, lack accessory salivary glands and an anal gland, and confine torsion of the alimentary system to the region of the mid-oesophagus between the valve of Leiblein and the duct from the gland of Leiblein (Ponder 1973a). The head-foot is red to orange, the stomach lacks a caecum, the pallial oviduct lacks an ingesting gland, and the pallial sperm duct lacks a distinct prostate gland and does not open to the mantle cavity (Marcus, Ev. & Marcus, Er. 1962; Ponder 1970c, 1973a). Fascioliariids are most readily recognised by their characteristic radulae, consisting of narrow, tricuspidate central teeth, that may be reduced to a single cusp in gerontic individuals of some species (Hollister 1954), and broad, multicuspidate lateral teeth in which the innermost cusp is usually the largest and the number of cusps increases with increasing shell size (Hollister 1954; Paine 1966; Maes 1967; Bandel 1984).

The family is here divided into three subfamilies, the Fascioliariinae, Peristerniinae and Fusininae, primarily on the basis of shell characters. This is a tentative arrangement pending availability of further information, particularly on anatomy. Fascioliariines are recognised by their tortuous columella with a prominent siphonal fold and two oblique plaits. They tend to inhabit shallow water sand substrata, and many are burrowers. Peristerniines have heavy, strongly ribbed, nodulose shells that are often pseudo-umbilicate. The columella has three transverse plaits in addition to a reduced siphonal fold. Species are subtidal and epifaunal, inhabiting rocks and reefs. Fusinines lack columellar folds and have a long, axial, non-umbilicate siphonal canal. Most species are subtidal burrowers.

The Fascioliariidae appear earlier in the fossil record than the Buccinidae, Melongenidae or Nassariidae, with the first fossil occurrences in the Aptian of the Lower Cretaceous (Taylor, J.D. *et al.* 1980). The family is well represented during the Tertiary (Grabau 1904). In the Recent fauna, fascioliariids occur in temperate to tropical regions, primarily at subtidal continental shelf depths, but with several species in the bathyal zone (see for example, Ponder 1970c).

The diet of smaller fascioliariid species consists of polychaetes, whereas bivalves and gastropods comprise an increasing fraction of the diets of larger species in proportion to their size (Paine 1966; Taylor, J.D. 1978b). Cannibalism has been reported in some species (Wells, F.E. 1970; Snyder & Snyder 1971).

Fascioliariids are gonochoristic. Fertilisation is internal, with 40 to 2100 eggs deposited in leathery, vase-shaped, stalked capsules with a flat to concave apical region containing the preformed hatching aperture. Capsules are attached to a hard substratum, including shell fragments, and occur in large clusters that may be communal (D'Asaro 1970a, 1970b; Bandel 1976b). Only five to 61 larvae emerge from each capsule, having consumed the remaining nurse eggs. Development is usually direct, and has been the subject of a few detailed studies (Osborn 1904; Glaser 1907; Gohar & Eisaway 1967).

The family Fascioliariidae is well represented in Australian waters. The more common shallow-water species are reviewed and figured by Wilson & Gillett (1971). Those from northern Queensland are discussed by Loch (1978). Wilson (1994) described and illustrated the shells of many fascioliariid species from Australian waters, in the subfamily Fascioliariinae.

Family Volutidae

Commonly known as volutes or bailer shells, these marine snails are small to large (9–500 mm) with a highly coloured, smooth to strongly sculptured, narrow to globose shell with a high to sunken spire.

In the past, members of families such as the Volutomitridae, Costellariidae and Mitridae were included with the volutes because of their general similarity in shell characters. As more anatomical information became available, the family Volutidae was eventually defined in the way we now know it. The most recent revisions of extant species are by Weaver & du Pont (1970) and Poppe & Goto (1992). Darragh (1989) has revised most of the Australian genera, some of the living species and all the fossil species. The extant Australian species are illustrated by Wilson (1994).

The shell is dextral, ovate to fusiform, sometimes involute, sometimes highly coloured, often with elaborate patterns and often coated with a smooth, highly polished glaze, or (rarely) having a brown periostracum (Fig. 15.164A–F). The protoconch is generally smooth, and is sometimes multi-whorled, but is generally of one to three whorls, the first of which may be bulbous and deviated from the axis of the shell. Also, the protoconch is usually calcareous, but is horny and deciduous in some groups. The aperture is elongate, usually about a third the length of the shell and produced into a short but well defined anterior canal. A siphonal notch and fasciole are usually present, and vary in degree of development. Columellar plaits are usually present, variable in number, generally ranging from three to five, sometimes with numerous weaker plaits inserted between and posterior to the stronger plaits. The mantle, siphon, proboscis sheath and foot are highly coloured, sometimes complementing the colour pattern of the shell.

The foot is broad and large (Pls 28.4, 28.5) and an operculum is present in only a few genera (for example, *Lyria*). The head is small, wide and flattened, usually with a large central lobe that is divided in some groups, for example *Lyria*, and *Athleta* (*Ternivoluta*), by a median cleft, and has two lateral lobes on which are situated two flattened triangular tentacles. The eyes, if present, are small and usually behind and at the base of the tentacles. The inhalant siphon is large and overlies the head with one, as in *Lyria* and *Athleta* (*Ternivoluta*), or, more generally, two appendages at its base. The mantle, in a few genera, is large and capable of enveloping the shell.

As far as is known all volutids are carnivorous, mostly feeding on other molluscs which they envelop with the foot (Morton, B. 1986b). Some deep-water forms (*Livonia*) prey on echinoderms (T. Darragh personal observation).

The anatomy has been studied in detail in only a few non-Australian species (Clench & Turner 1964; Ponder 1970b; Harasewych & Kantor 1991), though McMichael (1960, 1964) and Darragh (1989) have made a few observations on some Australian species, and some anatomical information on extralimital taxa has also been provided by Arnaud & Van Mol (1979) and Leal & Bouchet (1989). The radula (Fig. 15.164G, H) is rachiglossate, usually uniserial with tricuspidate, or rarely (*Amoria*) unicuspidate teeth (McMichael 1964), except in *Athleta* (*Ternivoluta*) which has a triserial radula with a central row of small tricuspidate teeth and small unicuspidate laterals (McMichael 1960). Part of the alimentary tract is illustrated in Figure 15.164I. Salivary glands are of two types, the tubular accessory salivary glands, which may be short or very long, and the racemose or normal salivary glands which are usually large.

15. PROSOBRANCHS

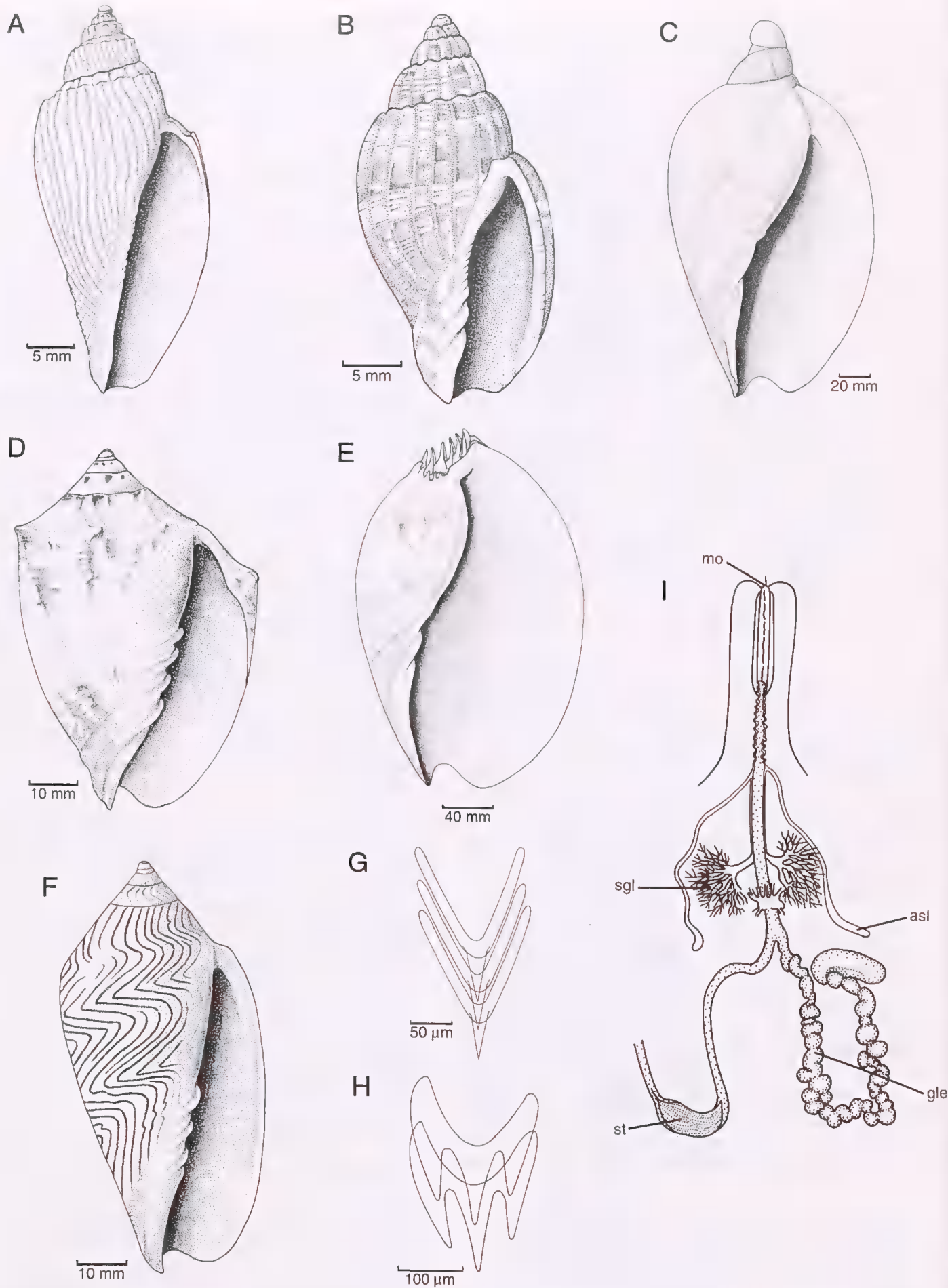


Figure 15.164 Family Volutidae. A–F, shells, apertural view: A, subfamily Athletinae, *Athleta* (*Ternivoluta*) *studeri*; B, subfamily Lyrinae, *Lyria* *mitraeformis*; C, subfamily Fulgorariinae, *Livonia* *mamilla*; D, E, subfamily Cymbriinae, D, *Cymbiola* (*Aulica*) *flavicans* and E, *Melo* *umbilicatus*; F, subfamily Scaphellinae, *Amoria* *undulata*. G, H, radular teeth: G, *Amoria* *lineata*; H, *Cymbiolacca* complexa. I, *Voluta* *musica*, digestive system, dorsal view. asi, accessory salivary gland; gle, gland of Leiblein; mo, mouth; sgl, salivary gland; st, stomach. (G, after McMichael 1964; H, after McMichael 1959; I, after Clench & Turner 1964)

[A–F, S. Weidland; G–I, C. Eadie]

The gland of Leiblein is muscular, long, tubular and convoluted, and has an apical bulb. The hypobranchial secretion is sometimes purple as in the Mitridae and Muricidae. The kidney has the primary and secondary lamellae separated. Sexes are separate. The pallial part of the vas deferens may be a groove in the body wall or be completely buried in it. The penis is generally very long and recurved.

Spawn varies within the family from solitary horny or calcareous capsules to complex egg masses comprising many capsules. Egg masses consist of clusters of leathery capsules cemented together, row upon row, forming a more or less rectangular mass, which in some *Melo* species can be over 400 mm long. The egg masses are usually attached to hard, fixed substrata such as dead shells, dead coral or even sticks, and other mud-lodged debris. One African genus, *Cymbium*, broods embryos in a special pedal pouch. From each capsule only one embryo develops to maturity, even though, initially, several embryos may have been present (Marché-Marchad 1968). The eggs of *Melo* species develop directly into the crawling stage (Allan & Middleton 1946) as do most volutes (Penchaszadeh 1988). All volutids produce large egg capsules containing few eggs. The embryos grow, sometimes over several months, the juveniles, on hatching, sometimes being very large (sometimes greater than 10 mm). In many volutes extravitelline food consists of albumen, nurse eggs being absent (Penchaszadeh 1988). There are a few fossil species which have a multispiral protoconch, suggesting that they have a pelagic larval stage. Direct development in Recent taxa has resulted in many locally distinct populations and often a hazy delineation of species-group taxa, as with for example, the *Cymbiola pulchra* group from Queensland.

Volutes are found throughout the oceans of the world, particularly in the Southern Hemisphere, but none has been found in Europe or along the Atlantic coast of North America. They range from shallow, littoral areas to the abyssal depths, though most live and burrow in sand in sublittoral areas. Surprisingly little is known about the biology of this important and conspicuous family, yet it is among the most popular with shell collectors.

Australia has the greatest diversity of genera and about one third of the described extant species. Though up to 38 generic names have been used for Australian volutes by some authors, only 18 are considered distinct by Darragh (1989) and five of these are known only as fossils. Volutes occur Australia-wide. *Amoria* and *Melo* have a circum-Australian distribution. *Cymbiola* and *Volutaconus* are found in tropical and subtropical regions and *Lyria* has a relict distribution in the West Pacific and Indian Oceans and the Western Atlantic, vestiges of a former cosmopolitan distribution. *Athleta* had a cosmopolitan distribution in the Tertiary, but now occurs only in the Indian and Atlantic Oceans off South Africa.

The major portion of the living fauna is descended from the fossil fauna of the Tertiary of south-eastern Australia. The oldest known member is the cosmopolitan *Athleta* (*Athleta*), known only from the Palaeocene of Victoria (Darragh 1971). The endemic subgenus *Athleta* (*Ternivoluta*) (Fig. 15.164A) first occurs in the late Eocene of Victoria along with the endemics, *Notovoluta*, *Ericusa* and *Notopeplum*, which extend through to the present. Restricted to the Late Eocene are *Mitreola*, related to European Palaeogene species and American Neogene and Recent species, and *Scaphella* (*Aurinia*), a cosmopolitan group occurring in the Palaeocene to Pliocene of Europe and Miocene to Recent of North and Central America. The predominantly New Zealand genus, *Alcithoe*, is represented in the Late Eocene and Late Pliocene. The once cosmopolitan *Lyria* (Fig. 15.164B) made its first appearance in the Late Oligocene of Victoria along with the endemics *Livonia* (Fig. 15.164C) and *Nannamoria*, and with *Cymbiola* (Fig. 15.164D), which is related to Tethyan species in the Late Miocene of Indonesia. *Leptoscapa*, known in Australia only from a single species that ranges from Middle Miocene to Recent, is present in the Middle to Late Eocene of Europe and in the Late Eocene of Java. The only fossil records of *Melo* (Fig. 15.164E)

and *Volutaconus* are in the Middle Miocene of Western Australia. The endemic *Amoria* (Fig. 15.164F) first occurs in the Late Miocene of Victoria. *Lyrenaeta* has no known fossil record.

Family Olividae

This family of marine gastropods is usually found in shallow water in all the tropical seas of the world and in the southern temperate seas. Deep-water species are known and in Australia there are a few species found at 400 m, for example *Amalda hilgendorfi*. The shells are mainly subcylindrical or subfusiform, usually solid, porcellaneous and small to moderate in size (rarely over 100 mm in length).

The family is divided into four subfamilies. The Olivinae, the true olives, are common in the tropical waters of northern Australia; one species, *Oliva australis*, occurs on the southern coast. The Ancillinae are widespread in tropical and temperate seas, and although they may not be abundant in Australian waters they are diverse (Kilburn 1977, 1981). The Olivellinae consists of mainly small species, several of which are common in tropical and subtropical coastal waters of Australia (Iredale & McMichael 1962). The Pseudolivinae are represented by the genus *Zemira* in south-eastern Australia (Ponder & Darragh 1975). Accounts of the family include those of Ev. Marcus & Er. Marcus (1959a, 1959b), Macpherson & Gabriel (1962), Zeigler & Porreca (1969) Wilson & Gillett (1979), Petuch & Sargent (1986) and Wilson (1994). Recent cladistic analysis based on anatomical studies (Kantor 1991) has indicated that this group should be divided into the families Pseudolividae, Olividae and Olivellidae, placed in two separate superfamilies. This is not followed here as more work is needed for confirmation of these proposals.

The shells are dextral and of two main forms (Fig. 15.165A–D). The true olives are solid and cylindrical with a low spire (Fig. 15.165A) and a long narrow aperture with several strong columellar plaits. They have a very high gloss, are often highly coloured and are variable in colour and pattern. Adults lack an operculum; members of the other three subfamilies have a thin, horny operculum. Olivellines have a smaller shell with a higher spire than olivines, but the shell is almost as solid and glossy. Ancillines have a thinner, less glossy, usually fusiform shell with a wider aperture and higher spire (Fig. 15.165B). Often the sutures are covered with callus. Most of the shell is smooth but a sculptured anterior zone, the 'fasciolar band', is marked by an incised groove or raised ridge. This zone or band may be wide or narrow, smooth or grooved. In *Zemira* (Fig. 15.165C), the shell has a paucispiral protoconch and an ovate teleoconch, usually spirally grooved with a tooth on the outer lip behind which a prominent spiral groove is impressed on the middle of the base. The anterior siphonal sinus is wide and deep and the posterior sinus is not distinct. The umbilicus is moderate to absent. The operculum is large and oval, with a subterminal nucleus (Fig. 15.165C).

The head is small and poorly defined with concealed or reduced tentacles. The foot is large and separated by a deep transverse furrow into an anterior shield-shaped propodium and a posterior metapodium, the sides of which can be expanded over the shell (Fig. 15.165D, E; Pl. 29.2). In *Oliva*, the oral flaps bear tentacles with well-developed eyes, and both *Oliva* and *Olivella* have an anterior mantle tentacle. Most groups have a posterior mantle tentacle which lies in the channelled suture. Clusters of sensory cells lie under the epidermis of the anterior border of the propodium. The pedal gland is associated with the transverse ventral furrow.

The radula of all olivids is typically stenoglossate with a broad central tooth with three or more cusps, and broad based, arcuate lateral teeth (Fig. 15.165F). The foregut in *Oliva* is similar to that in muricids (Marcus, Ev. & Marcus, Er. 1959b), the stomach is highly differentiated with a gastric shield, and the anal gland opens behind the anus. *Olivella* has true salivary glands with no valve or gland of Leiblein. A large part of its stomach is cuticularised and acts as a gizzard. *Olivella* has no anal gland.

15. PROSOBRANCHS

The central nervous system in *Olivella* shows distinct separation of the ganglia with fairly long inter-ganglionic connectives. This makes it possible for the oesophagus and nerve ring to be distended when the animal swallows entire bivalves. The ganglia of *Oliva* are almost touching with very short connectives forming a rigid nerve ring. This only permits limited distension of the oesophagus, the animals feeding on small fragments rasped from the prey, or small animals or liquefied food (Marcus, Ev. & Marcus, Er. 1959b).

A female gono-pericardial duct is present and the remains of a male gono-pericardial duct are seen in the form of a diverticulum of the pericardium ending blindly at the renal sperm duct. A proximal appendage of the pallial oviduct functions as a seminal receptacle in *Oliva* and *Olivella* (Marcus, Ev. & Marcus, Er. 1959b). The kidney is a simple, unlobed organ.

Ponder & Darragh (1975) described the main features of *Zemira* and placed it in the Pseudolivinae. The head bears a pair of short, broad, flattened tentacles, the outer lobes of which bear small eyes. The foot is short, broad and rather thin with no dorsal outgrowths or transverse groove, but the anterior half is observed to contract to form a deep groove running to the anterior margin which may be used to hold prey during feeding. The anterior mucous gland opens to a slit along the anterior margin of the foot. There are no pallial tentacles. The mantle cavity contains a large, long osphradium, a large ctenidium with long, narrow filaments and a hypobranchial gland that occupies the right posterior part of

the cavity roof. The hypobranchial secretion is colourless and does not turn purple on exposure to light, as has been observed in several neogastropod families. The proboscis is very short; the salivary glands open by short free ducts into the buccal cavity and there are no accessory salivary glands. The intestine is a broad tube; anal papillae are absent, but a short anal gland is present. The ganglia of the central nervous system are concentrated with very short connectives as in *Oliva*.

Most members of the family are sand-dwelling carnivores or scavengers. Olsson & Crovo (1968) described the feeding behaviour of captive *Oliva sayana* when given both dead and living prey. Ev. Marcus & Er. Marcus (1959b) described *Olivella verreauxii* capturing and ingesting whole large bivalves. They also reported foraminiferans, copepods, amphipods and scaphopods as stomach contents of this species, though since bivalves are its principal food, these may have been from the stomach of the bivalve. Olivids usually burrow through the sand with the propodium and one species, the ancillid *Ancillista cingulata*, has been recorded swimming by Wilson (1969), probably as an escape reaction. Ev. Marcus & Er. Marcus (1959b) recorded *Olivella verreauxii* swimming by means of its wing-like metapodial flaps and this has also been observed in *Cupidoliva nympha* (W.F. Ponder personal communication).

Olsson & Crovo (1968) recorded *Oliva sayana* laying clear jelly, spherical egg capsules free on the surface of the sand, each capsule containing 20 to 25 yolky eggs. All these eggs developed,

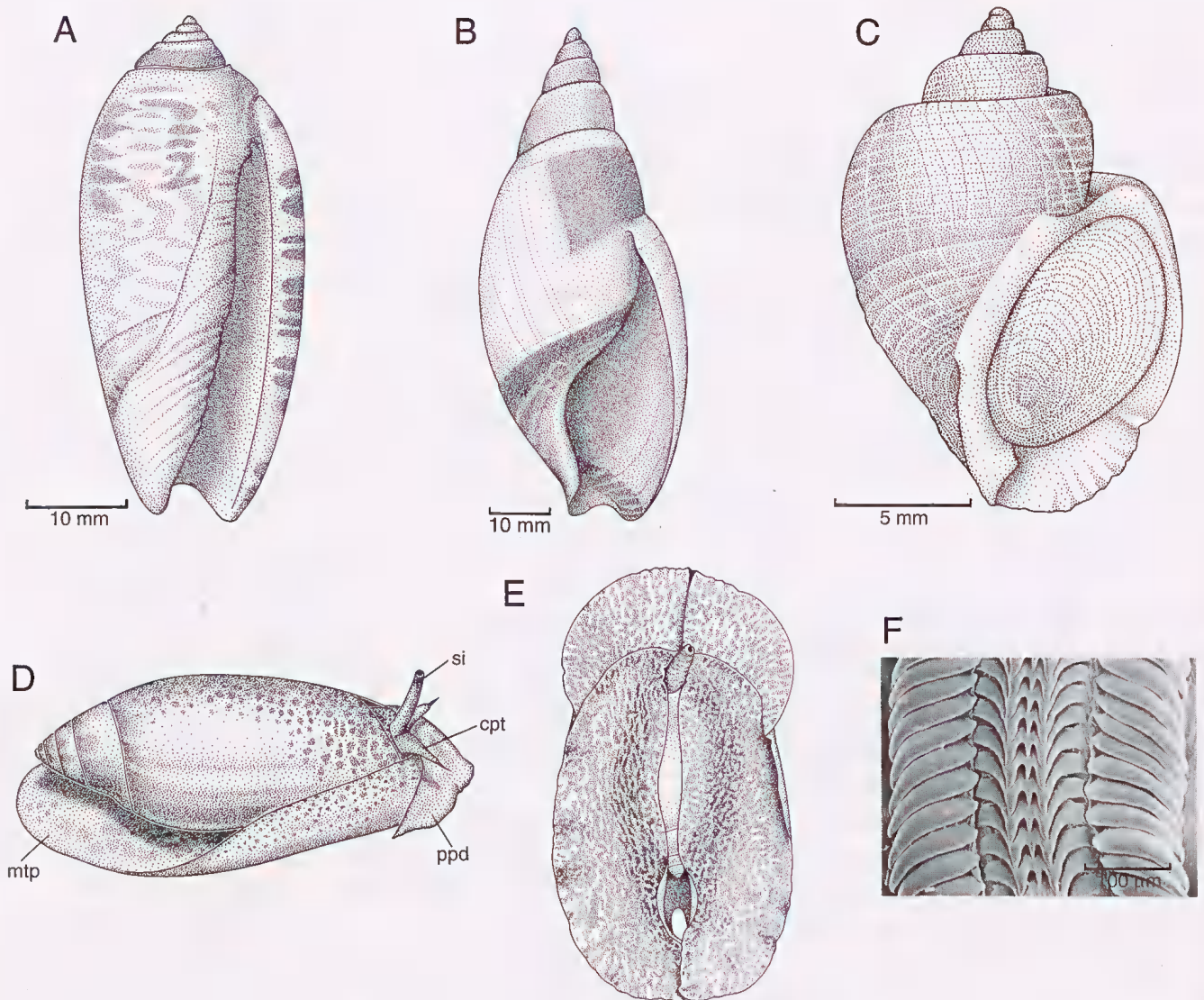


Figure 15.165 Family Olividae. A–C, shells, apertural view: A, subfamily Olivinae, *Oliva caerulea*; B, subfamily Ancillinae, *Ancillista velesiana*; C, subfamily Pseudolivinae, *Zemira australis*, with operculum closing the shell aperture. D, *Oliva australis*, crawling with the siphon extended; E, *Ancillista cingulata*, dorsal view. F, *Oliva miniacea*, several transverse rows of radular teeth. cpt, cephalic tentacle; mtp, metapodium; ppd, propodium; si, siphon. (D, after photograph by N. Holmes; E, after photograph in Wilson & Gillett 1971)

[A–E, C. Eadie; F, B.J. Smith]

the free-swimming veligers being liberated into the water after three to five days. Ev. Marcus & Er. Marcus (1959b) recorded *Olivella verreauxii* laying egg capsules attached to the substratum; these liberated free-swimming veligers which fed on yolk for the first few days and then settled.

Members of the family are found in all the tropical and subtropical regions of the world (Petuch & Sargent 1986) and a few species are also found in the cooler seas of southern Australia and New Zealand. The Australian fauna contains representatives of all four subfamilies. The genus *Oliva* is represented by about 14 species; the subfamily Olivellinae by the genus *Belloiliva* with about eight species in three subgenera; the subfamily Ancillinae by the genera *Amalda* and *Ancillista* with about 10 species and the Pseudolivinae by the genus *Zemira*, which is endemic to southern and eastern Australia. *Zemira* is recorded from as early as the Upper Eocene of Victoria (Ponder & Darragh 1975). Species of the subfamily Olivellinae are known from the Late Eocene through the Oligocene and Miocene of both Victoria and South Australia (Ludbrook 1953; Darragh 1985).

Family Harpidae

This is a small family of carnivorous marine gastropods with a globose to ventricose shell and a large last whorl. The shells are usually shiny and strikingly coloured and patterned. They have strong axial ribs and a short, deep, anterior siphonal canal (Fig. 15.166A–E). Australian species are medium to small (25–100 mm shell length) and are found in shallow to fairly deep water (2–200 m depth).

The extant species belong to three genera in two subfamilies: the Harpinae with the genera *Harpa* (nine species) from the tropical seas of the Indo-Pacific and central Atlantic and *Austroharpa* (four species) from western, southern and eastern Australia (Rehder 1973); and the Moruminae with the genus *Morum* (24 species) from the tropical and subtropical seas of the world (Emerson 1981, 1985) with three species being recorded from Australia (Beu 1976b). The two subfamilies differ in both shell and anatomical features. The shell of the Moruminae (Fig. 15.166D) has fewer nuclear whorls (1.5–2.5 vs 3.5–5), a narrowly constricted aperture with a widely flaring, dentate labrum and a large, raised parietal shield. It has a reduced operculum (harpines lack an operculum), a relatively smaller propodial shield, a less pronounced expansion of the mid-oesophagus, and radular teeth with relatively shorter cusps (Hughes, R.N. & Emerson 1987). The inclusion of *Morum* in the family was documented by R.N. Hughes (1986) and R.N. Hughes & Emerson (1987). Beu (1976b) and Emerson (1985) revised various Western Pacific species.

The harpine shell has a large, inflated last whorl, a short spire and acute apex, a broadly to narrowly ovate aperture and a well-marked siphonal notch (Fig. 15.166A). The sculpture is of strong axial ribs in *Harpa* (Fig. 15.166B) with spiral sculpture poorly developed. The shell is usually brightly coloured from reddish-brown to pink and often strikingly patterned with contrasting blotches. Many of the shells have a high glaze, particularly on the axial ribs where the glaze sometimes covers the penultimate whorl. There is no operculum. The animal is also often strikingly coloured and patterned. The head (Fig. 15.166E) bears slender, pointed tentacles with conspicuous external lateral eyes and a large siphon. The foot is large and fleshy and divided into a broad, flat propodium with lateral points which extend beyond the width of the rest of the foot or metapodium. The propodium is joined by a broad neck to the metapodium which is tapered to a point behind (Fig. 15.166E).

In *Morum* species, the shell has a long, narrow aperture extending the length of the last whorl, a short spire and a thickened and medially denticulate outer lip (Fig. 15.166D). It has cancellate sculpture of broad axial ribs and narrower spiral cords. The colour is usually dull with a whitish to buff background overlain by blotches or spiral bands of brown to tan. The parietal shield is commonly white, but is brightly coloured in some species, in

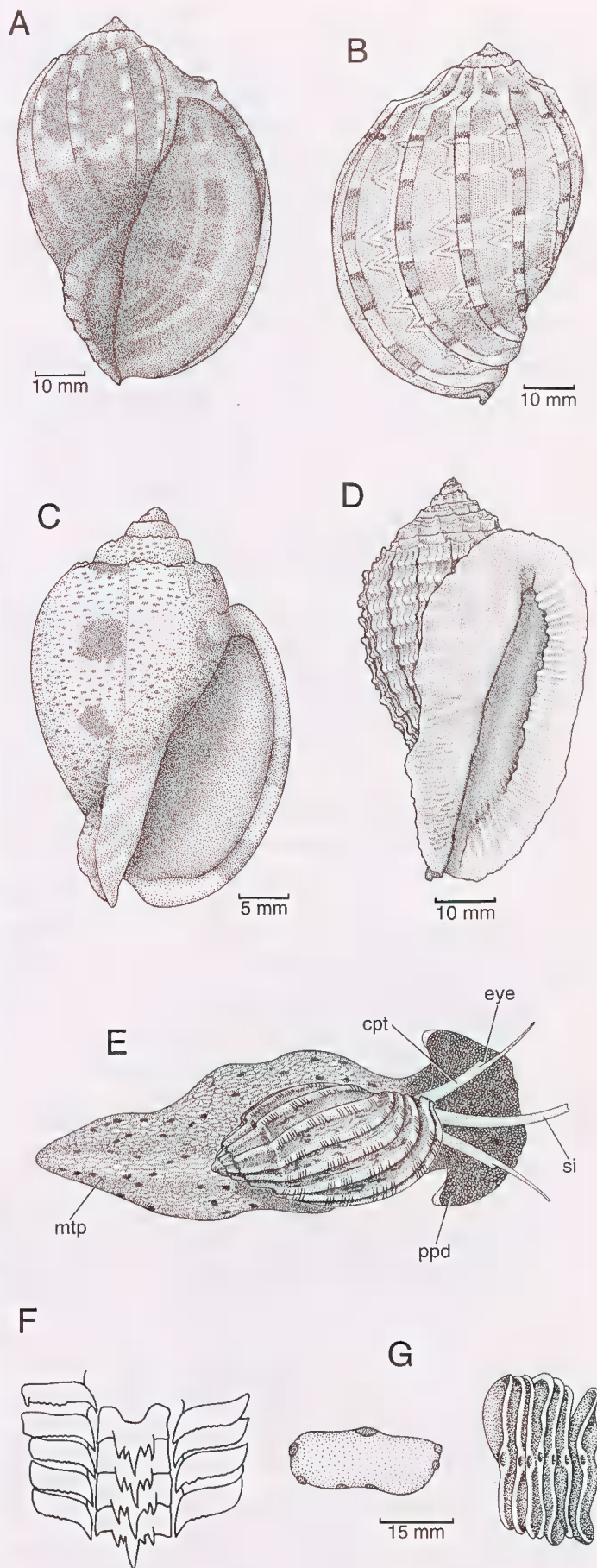


Figure 15.166 Family Harpidae. A, B, subfamily Harpinae, *Harpa articularis*, shell: A, apertural view; B, dorsal view, showing the shell pattern. C, subfamily Harpinae, *Austroharpa punctata*, shell, apertural view. D, subfamily Moruminae, *Morum grande*, shell, apertural view. E, F, *Harpa armouretta*: E, crawling animal; F, several transverse rows of radular teeth. G, *Harpa major*, egg capsules. cpt, cephalic tentacle; eye, eye; mtp, metapodium; ppp, propodium; si, siphon. (E, after Wilson & Gillett 1971; F, G, after Rehder 1973) [C. Eadie]

15. PROSOBRANCHS

shades of red, orange or purple. The propodial shield is slightly shorter than in *Harpa* (Fig. 15.166E). An elongate operculum is present, the subcentral nucleus with fine concentric lines on its outer surface.

The internal anatomy of the two subfamilies is very similar. The siphon opens onto a large, bipectinate osphradium. The ctenidium is large and the hypobranchial gland is well developed, producing copious amounts of mucus but no coloured secretion. The buccal mass and radula are microscopic, the radula being only about 2.5 µm wide in large specimens, consisting of a single column of tricuspidate or multicuspidate teeth with, in some species, a lateral tooth or tooth plate (Fig. 15.166F). It is so small that it was thought for a long time that the radula was lost in adults. *Morum* has relatively shorter tooth cusps than *Harpa*. Much of the cephalic haemocoel is occupied by the two large salivary glands. The ducts open into the buccal cavity, so do not pass through the nerve ring. There are no accessory salivary glands, and no gland or valve of Leiblein. The mid-oesophagus is wide in the Harpinae, less so in *Morum*, and lined by extensively folded epithelium. The posterior oesophagus and stomach are narrower and similarly folded. The rectum lacks an anal gland. The central nervous system is a compact ring with very short commissures which allows little expansion of the anterior oesophagus.

Harpa species feed on fairly agile brachyuran crustaceans and *Morum* species probably feed on slower moving anomuran crustaceans (Hughes, R.N. & Emerson 1987). The crabs are enveloped by the propodium and metapodium and imprisoned by copious quantities of mucus. The microscopic radula penetrates the thin arthrodial membranes of the crustacean prey, and saliva containing digestive components is injected with the aid of the highly muscular salivary ducts. The semi-digested fluid is then withdrawn with the aid of the muscle strands in the wall of the wide mid-oesophagus which may serve as a dilatable pump for the ingestion of fluid (Hughes, R.N. 1986). The kidney is pycnonéphridial.

Sexes are separate. The male has an elongate, tapering penis on the right anterior side of the head and an open or closed distal vas deferens. There is a slight size dimorphism, the shells of males being somewhat narrower than those of females. Details of egg capsules and laying procedure are given for two species of *Harpa* by Rehder (1973). The female attaches the egg mass to a rock or other hard surfaces. The egg mass consists of about 11 to 15 flattened, rubbery rectangular capsules (Fig. 15.166G), about 15–20 mm by 30–40 mm, attached to each other by about six points of attachment so that the mass looks like a loose stack of plates. Each capsule has a transparent pore at the top edge covered by a thin membrane and each capsule contains about 3000 to 4000 minute eggs. These are thought to develop to veliger stage before being released into the plankton (Hughes, R.N. & Emerson 1987). Egg masses of *Morum* consist of about eight capsules joined in a row by a basal membrane cemented to a rock. *Morum oniscus* lays its eggs beneath small slabs of coral-rock at low-tide level (Work 1969). The capsules are broadly triangular, with one face convex and covered with blunt spines. Each capsule has a subapical escape aperture on the concave side and contains between 10 to 15 yolky eggs. These undergo direct development, taking about 30 to 35 days, and go through a veliger stage in the capsule. They hatch as crawling young (Work 1969; Hughes, R.N. 1990). The spawn and development of *Austroharpa* are unknown. The protoconch morphology suggests direct development.

Members of both subfamilies autotomise the posterior end of the foot when disturbed. This is possibly an escape response to predation, probably by large fishes. Nothing is known of the ecology or behaviour of members of the rarer, deep-water genus *Austroharpa*.

The Australian fauna consists of four species in the genus *Harpa*, four species of *Austroharpa* (*Palmaharpa*) (Rehder 1973) and three species of *Morum* (Beu 1976b), all of which are uncommon to very rare.

Members of the family are widespread as fossils. They are fairly common in some Tertiary deposits in Europe, North and South America, Asia, Australia and New Zealand. The most widespread genus, *Eocithara*, probably ancestral to *Harpa*, has one Australian species, *Eocithara (Refluharpa) lamellifera*, from the Middle Miocene of Victoria. By contrast nine species in two subgenera of *Austroharpa* are known from a wide range of Tertiary sites in Victoria and South Australia (Rehder 1973).

Family Marginellidae

These small marine snails (Pls 28.1, 28.2) typically have a shell with a short to sunken spire, a large last whorl, columellar plaits and a smooth, polished surface. The radula has only the central teeth present in the majority of genera and is absent in others. The sometimes brightly coloured mantle is usually capable of covering all or part of the shell and the large foot lacks an operculum. Since this account was written, Coovert & Coovert (1995) have divided the Marginellidae into two families, Cystiscidae and Marginellidae.

Marginellids have a distinct, but rather uniform shell form making delineation of genera difficult. The first major revision of Australian species was by Tate & May (1900) who simply listed the Tasmanian species and placed them all in *Marginella*. Cotton (1944, 1949) arranged the Australian species in species groups, but Laseron (1957) was the first to refer the Australian species to different genera. In all, Laseron created 33 genera, for the fossil and extant species, but he did not recognise the genus *Marginella* in Australia. Coan (1965) proposed a reclassification of the Marginellidae, suppressing many of Laseron's genera in synonymy. There is still no adequate generic classification of the Marginellidae, as only shell characters have been used to define many genera and still nothing is known of the animal, radula or anatomy of some critical species (see Coovert & Coovert 1995 for recent review).

The shells of Australian species are less than 20 mm in length, although some marginellids reach 120 mm. They are biconic or ovate with a paucispiral protoconch, and a moderately long to involute spire (Fig. 15.167A–D). The shell is usually smooth and glossy. Sculpture, if present, is usually limited to axial plications restricted to the shoulder, although a few species have surface granulation. The aperture is flaring to narrow, with several (two to 12, usually three to four) strong plaits on the columella, there is no umbilicus and the outer lip has an external varix and is smooth or denticulate internally. The anterior apertural canal is short and not siphonate, narrow to broad, and the posterior canal is absent or poorly developed.

Space does not allow a full listing of the genera, but some of the more important are described briefly. *Austroginella* species have a shell with a thickened outer lip bearing a strong varix. The columella has four very strong plaits. *Ovaginella* has an ovate shell with an involute spire, and has four strong plaits on the lower third of the columella. The outer lip is thickened and has a weak varix. Species of *Cystiscus* have a small, generally ovate, shell with a flattened or involute spire, and more than four relatively weak plaits on the columella that extend the whole length of the aperture; the outer lip is usually thin. Another genus, *Mesoginella*, has a narrow, elongate shell as in *Austroginella*, with four plaits on the columella. The outer lip of the peristome is thickened and usually with a slight varix. Species of *Haloginella* have a cylindrical shell with a short spire; the outer lip is varicose and smooth to minutely denticulate inside. The columella has four plaits and the shell has brown spiral bands.

The foot is broad and usually longer than the shell (Figs 15.167I, J, 15.168A). The external features of the animal divide marginellids into two groups that have, very recently, been treated as full families by Coovert & Coovert (1995). They recognise the Marginellidae as comprising taxa with unmodified internal whorls, and columellar plications continuous internally. The radulae are shorter and broader, odontophoral cartilages are

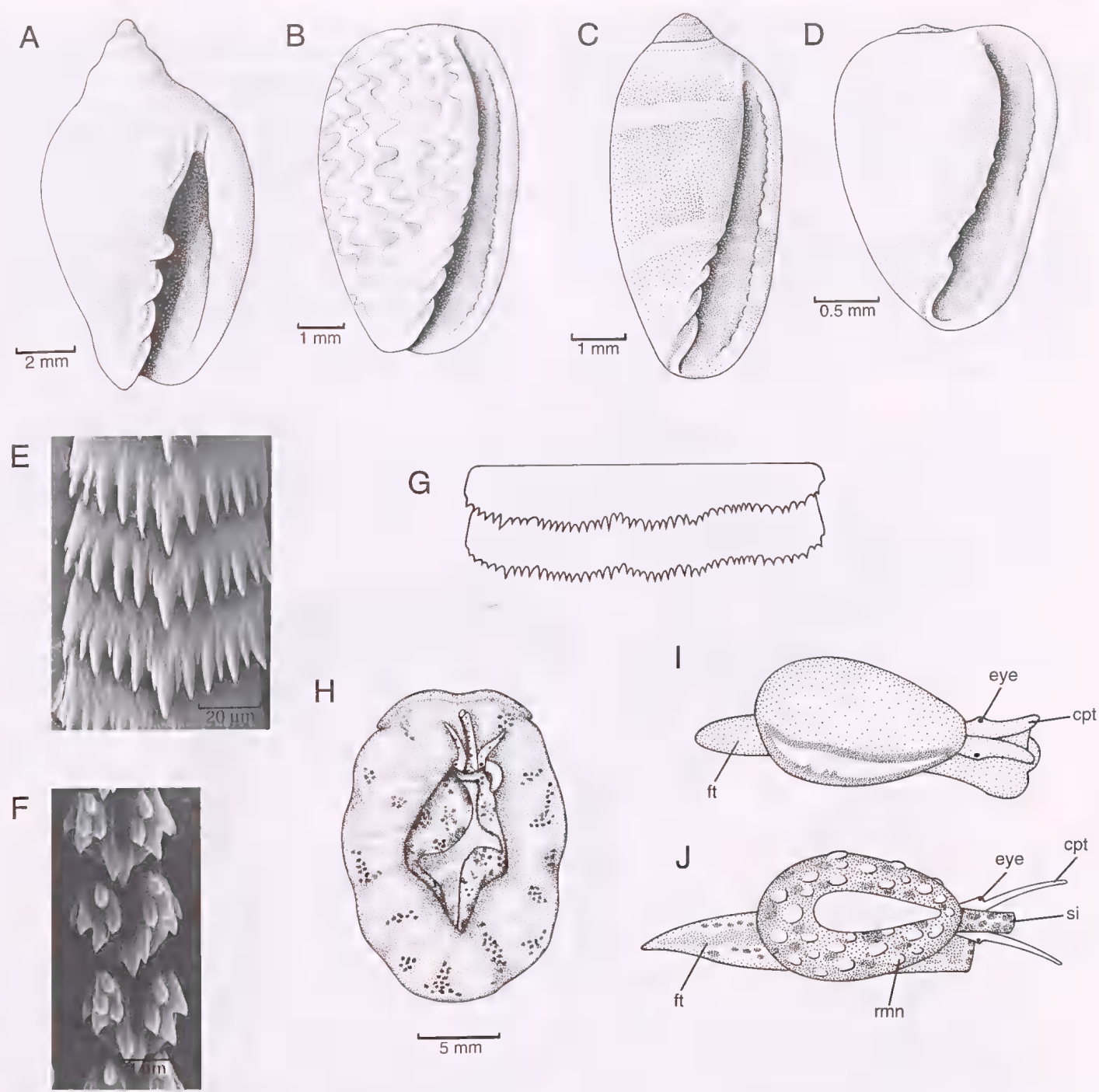


Figure 15.167 Family Marginellidae. A–C, subfamily Marginellinae, shells, apertural view: A, *Austroginella muscaria*; B, *Persicula pulchella*; C, *Haloginella mustellina*. D, subfamily Cystiscinae, shell, apertural view: *Cystiscus angasi*. E–G, several transverse rows of the radula, only one tooth in each row: E, *Marginella johnstoni*; F, *Pugnus parvus*; G, *Haloginella mustellina*. H–J, crawling animals, dorsal view: H, *Austroginella johnstoni*; I, *Cystiscus angasi*; J, *Granulina nympha*. cpt, cephalic tentacle; eye, eye; ft, foot; rmn, reflected mantle lobe reflected over shell; si, siphon. (G, after Coovert 1986; H, after photograph in Murray 1959; I, J, after Lasern 1957) [A–D, S. Weidland; E, F, Australian Museum; G–J, C. Eadie]

fused anteriorly and a special buccal pouch is present in which the odontophore lies. The other group, the Cystiscidae, which Coovert & Coovert (1995) consider to be more closely related to the Olividae, have internal shell whorls partially resorbed and columellar plications reduced internally. The radular morphology differs. The teeth are narrower and more numerous, the subradular membrane structure differs, the radular sac is typical, and the odontophoral cartilages are separate. In typical marginellids, the siphon and tentacles are long and narrow (Figs 15.167J, 15.168A), and in ‘cystiscids’ the tentacles and siphons are fused forming a head that appears to be bifurcate (Fig. 15.167I). The eyes are on swellings at the base of the tentacles. The foot and mantle are often brightly coloured and the mantle is usually capable of covering the shell, or at least part of it, and may be decorated with blister-like structures. In the mantle cavity there is a large, bipectinate osphradium and a somewhat narrower ctenidium with broadly triangular filaments.

The feeding habits of marginellids are not well known. Some feed on bryozoans, others are known to feed on ascidians. In all probability they feed on a wide range of animal food, although each group may feed selectively on one type of food. At least one species is known to be parasitic on fishes, feeding on them while they rest in cavities in coral at night (Kosuge 1986; Bouchet 1989). Two sand-living species of *Austroginella* are known to drill holes in small bivalves and feed on their flesh (Ponder & Taylor 1992). This is the only record of shell drilling in the Marginellidae but it is probable that at least some other related species are capable of it.

The alimentary canal (Fig. 15.168B–D) has a (usually short) proboscis, a pair of salivary glands, a pyriform valve of Leiblein and a gland of Leiblein that is similar in morphology to the toxoglossan poison gland. The whole buccal mass is constricted from the buccal cavity, into a ventral buccal pouch. There is either

15. PROSOBRANCHS

a single accessory salivary gland or this structure is absent (Graham 1966; Ponder 1970a). Some genera lack radulae (for example, *Marginella*). The radula of all genera studied to date is characterised by the presence of only one tooth in each row (0–1–0) (Fig. 15.167G) with the exception of *Plesiocystiscus* which has a triseriate radula (1–1–1) (Coovert & Coovert 1995). The central tooth is a straight and narrow plate, or arched, and has multiple cusps (Bandel 1984).

The kidney in those species studied, is similar to that of the Volutidae and Olividae, and differs from most other muricoideans (Ponder 1970a, 1973a). The nervous system in the few species studied has the circumoesophageal ganglia extremely concentrated (Ponder 1970a).

Males have a prominent, elongate penis on the right side of the neck, behind the right cephalic tentacle. Sperm are stored in the seminal receptacle after mating occurs. Some species have an ingesting gland (Fretter 1976). Females produce large eggs that are usually laid singly in a capsule which is moulded by a gland in the foot. There are no nurse eggs, but there is a large supply of albumen which provides nourishment for the embryo. The egg capsules of only sixteen species are known for the family worldwide (Coovert 1986). Murray (1970) described the reproduction and life history of an Australian species, *Microginella minutissima* and illustrated the egg capsules which are laid on the host, *Amathia biseriata*, a colonial bryozoan. Marginellid egg capsules are of two types, both with a relatively

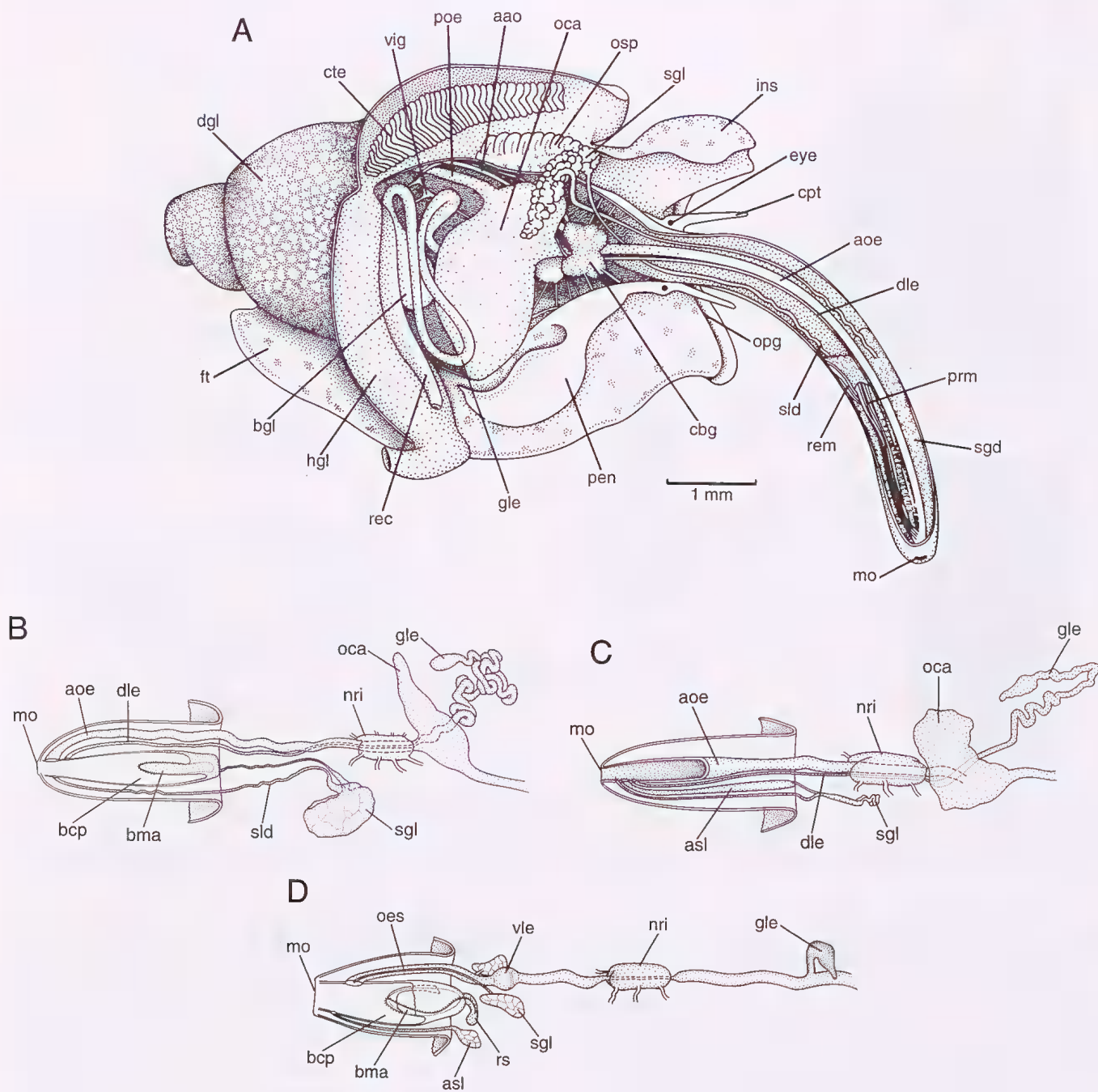


Figure 15.168 Family Marginellidae. A, *Volvarina taeniolata*, animal removed from shell, dorsal view, with the mantle cavity, visceral haemocoel and partly extended proboscis exposed by dorsal cut along the mantle skirt and body wall (glands have been removed to display the buccal pouch and retractor muscles of the proboscis are omitted). B–D, anatomical features of the foregut shown diagrammatically in lateral view: B, *Prunum* aff. *aletes*; C, *Hyatina pallida*; D, *Persicula interruptolineata* (= family Cysticidae, *sensu* Coovert & Coovert 1995). aao, anterior aorta; aoe, anterior oesophagus; asl, accessory salivary gland; bcp, buccal pouch; bgl, bulb of gland of Leiblein; bma, buccal mass; cbg, cerebral ganglion; cpt, cephalic tentacle; cte, ctenidium; dgl, digestive gland; dle, duct of gland of Leiblein; eye, eye; ft, foot; gle, gland of Leiblein; hgl, hypobranchial gland; ins, inhalant siphon; mo, mouth; nri, nerve ring; oca, oesophageal caecum; opg, opening of anterior pedal gland; osp, osphradium; pen, penis; poe, posterior oesophagus; prmu, protractor muscle of buccal pouch; rec, rectum; rem, retractor muscle of buccal pouch; rs, radular sac; sgd, subepithelial glands; sgl, salivary glands (paired); sld, salivary duct; vig, visceral ganglion; vle, valve of Leiblein. (A, after Fretter 1976; B–D, after Coovert & Coovert 1995)

[C. Eadie]

tough external capsule. The first type is lens-shaped or purse-shaped, compressed and fixed by a stalk. The second type is hemispherical and fixed by the flat base. The young snails emerge from the capsule at the crawling stage in all species studied.

Marginellids range from the lower intertidal zone to more than 1000 m in depth, and from rocky reefs to soft shores. One genus, *Rivomarginella* (Coomans & Clover 1972), is said to live in freshwater in Asia. In the temperate waters of southern Australia some species may be abundant. The somewhat confused taxonomy of this group does not allow a definitive biogeographic analysis. Some endemic genera occur in the Australian fauna, as well as some wide-ranging genera including: *Cystiscus*, *Persicula*, *Gibberula*, *Granulina*, and *Pugus* (= *Cystiseidae*, using the Coover & Coover 1995 classification) and *Serrata*, *Hydroginella*, *Alaginella*, *Mesoginella*, *Ovaginella*, *Balanetta*, *Volvarina* and *Dentimargo* (= *Marginellidae sensu stricto*). The only extant marginellid genus apparently restricted to Australia is *Austroginella*.

Several genera range from the Eocene to the present, including some in Australia, but marginellids also occur in the Upper Cretaceous of the United State of America (Sohl 1963). Australia has a rich Tertiary marginellid fauna (Cotton 1949), and its Recent fauna is the most diverse in the world.

Family Mitridae

These marine snails have solid, fusiform to cylindrical shells with an elongate aperture ornamented with columellar plaits. They lack an operculum. A diagnostic character for the family is a peculiar extensible epiproboscis through which the salivary ducts pass

(Fig. 15.169A). Other features that distinguish this family from the Volutomitridae and Costellariidae, which have similar shells, are the predominantly spiral sculpture, an anal gland, a ventral pedal gland in the female, a purple hypobranchial secretion and the lack of accessory salivary glands and the gland of Leiblein. The egg capsules are vase-shaped and the radula has multicuspitate lateral teeth (absent in one group) and relatively small, usually multicuspidate, central teeth.

Thiele (1929–1935), using Risbec's 1928 anatomical work as a basis, divided the Mitridae into three subfamilies, Mitrinae, Vexillinae and Cyndrininae. Cernohorsky (1966) followed Thiele's classification adding a new subfamily, Imbricariinae, his work based primarily on radular and shell characters. Ponder (1972a) examined the anatomy of the family and recognised two subfamilies, the Mitrinae (with Imbricariinae a synonym) and Cyndromitridinae (= Cyndrininae), with the Vexillidae (= Costellariidae) as a separate family.

Shells are small to large (5–170 mm) and have a high to low spire with a multispiral or paucispiral protoconch (Fig. 15.169A–C). The aperture is elongate, with a short, notched siphonal canal. The columella has two to 10 oblique folds of which the posteriormost fold is the largest. The surface is rarely smooth or polished and sculpture is predominantly spiral, consisting of grooves, striae, ribs, nodes, or pits; axial elements are weak or absent. The outer lip is usually smooth within and lacks a varix.

The foot is anteriorly truncate, and, in sand-dwelling species, can extend posteriorly beyond the apex of the shell. The mantle edge is simple and the colour pattern of the living animal is diagnostic

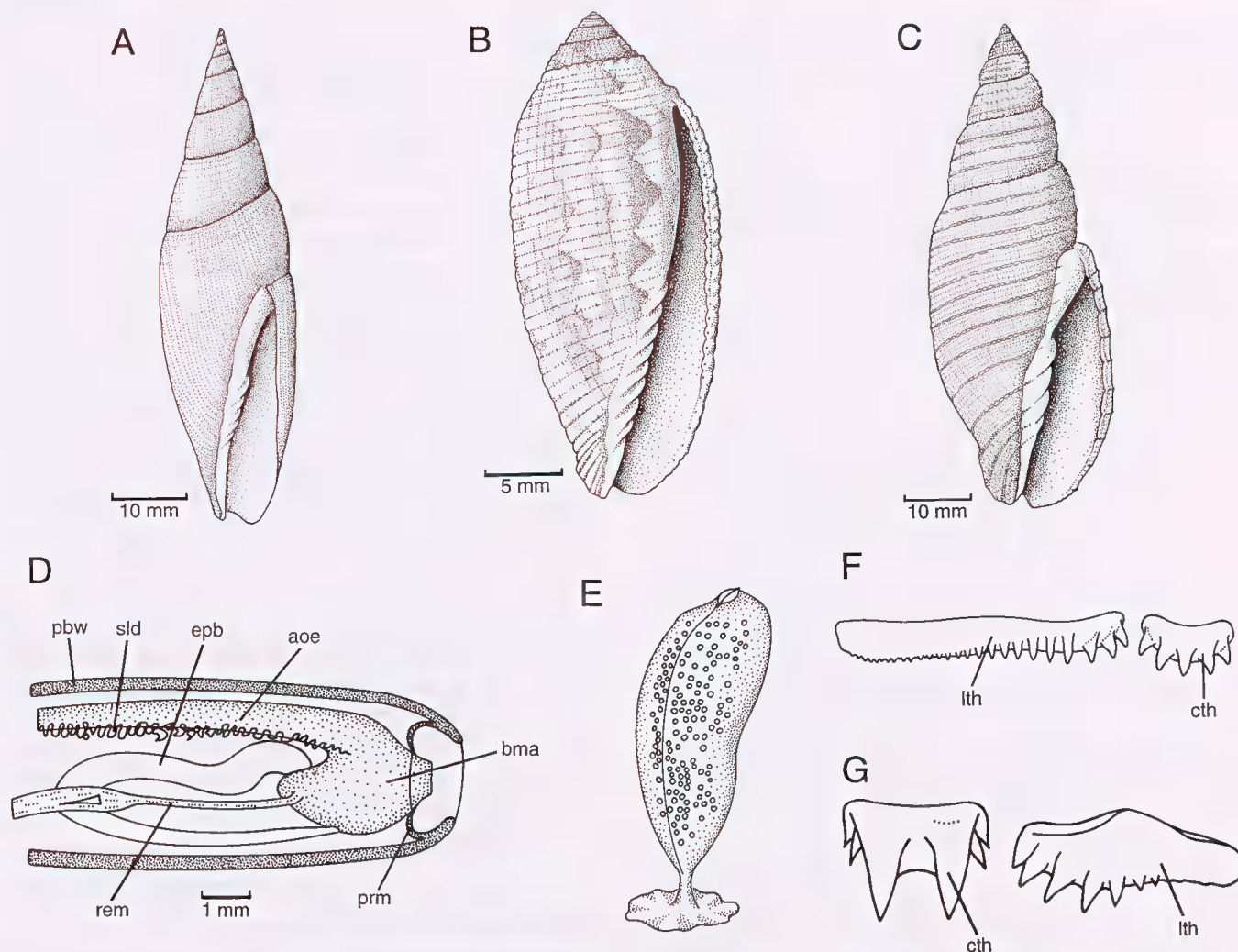


Figure 15.169 Family Mitridae. A–C, shells, apertural view: A, subfamily Mitrinae, *Mitra carbonaria*; B, subfamily Cyndromitridinae, *Pterygia crenulata*; C, subfamily Mitrinae, *Cancilla filaris*. D, mitrid anterior gut, lateral view, showing retracted epiproboscis. E, egg capsules of *Cancilla filaris*. F, G, radular teeth, central tooth with one of the lateral teeth: F, *Mitra papalis*; G, *Neocancilla papilo*. aoe, anterior oesophagus; bma, buccal mass; cth, central tooth; epb, epiproboscis; lth, lateral tooth; pbw, proboscis wall; prm, peristomal rim; rem, retractor muscle; sld, salivary duct. (D, after Ponder 1972a; E–G, after Cernohorsky 1970)

[A–C, S. Weidland; D–G, C. Eadie]

15. PROSOBRANCHS

for species, showing little variability. The cephalic tentacles are pointed, the eyes are at their outer bases, which are lengthened posteriorly as extensions of the tentacles.

The pallial cavity (Ponder 1972a) has a very large osphradium and a slightly longer ctenidium with triangular filaments. The hypobranchial gland is wedged between the ctenidium and the gonoduct. Some mitrids discharge a dark purple protective secretion from the hypobranchial gland when they are disturbed and, although this has no known harmful effects (on humans) it does have considerable staining properties.

Mitrids appear to feed exclusively on sipunculids (Taylor, J.D. 1989). The mouth is surrounded by a peristomal rim and the proboscis is large and long in the Mitrinae (Fig. 15.169D) and very long and narrow in the Cyndromitridinae. These two subfamilies also differ in radula structure, having a formula of 1-1-1 in Mitrinae (Fig. 15.169F, G) and 0-1-0 in Cyndromitridinae. The central tooth is usually small, rectangular and bow-shaped and multicuspidate. The lateral tooth (Mitrinae) is usually multicuspidate. The conspicuous epiproboscis is located in the buccal region (Fig. 15.169D) and carries the salivary ducts (Ponder 1972a; West, T.L. 1990, 1991). It gradually tapers anteriorly and when retracted is U-shaped. It is often longer than the odontophore. When extended it is inverted at its posterior end. T.L. West (1990, 1991) studied the function of the epiproboscis of two American mitrids that feed on sipunculids and suggested that the epiproboscis is an adaptation for feeding on soft-bodied, reclusive prey; the epiproboscis has been mistakenly referred to as a poison gland (Maes 1971; Cernohorsky 1970). The gland of Leiblein and accessory salivary glands are absent, but an anal gland is present. The kidney has the primary and secondary lamellae separated.

The gonad intermingles with the digestive gland, a feature not seen in the conchologically similar Volutomitridae or Costellariidae (Ponder 1972a). The male has a large pallial prostate gland and the penis has a closed duct. The female system is similar to that of other muricoideans (Ponder 1972a).

Rock-dwelling species deposit their egg capsules in loose asymmetrical clusters, on the underside of rocks and coral boulders. The egg capsules (Fig. 15.169E) are generally vase-shaped (15-100 capsules per cluster), and each capsule containing from 100 to 500 white to translucent yellow eggs. Free-swimming veliger larvae emerge from these capsules in many species (Cernohorsky 1970). Species with direct development presumably have fewer eggs in each capsule, but none has yet been studied.

The family is cosmopolitan, living in warm and temperate waters of both hemispheres. They are found on the undersides of rocks and coral boulders or buried in clean, muddy or silty sand. Most species (about 85%) live within the intertidal or shallow sublittoral zones; a few species live in deeper water.

Both subfamilies occur in Australia, the Mitrinae being by far the most conspicuous and diverse. Some genera in the Mitrinae have a circumtropical distribution, for example, *Mitra* (Fig. 15.169A) and *Cancilla* (Fig. 15.169C), both of which occur in Australia. According to Cernohorsky (1970), the genus *Mitra* has six subgenera of which five occur in Australia either as extant species or fossils. *Cancilla* comprises three subgenera all which occur in Australia either in the Recent or as fossils (Cernohorsky 1970). Species of the Cyndromitridinae, though often rare, are found in tropical Australia, the only genus being *Pterygia* (Fig. 15.169B). Pechar, Prior & Parkinson (1980) and Wilson (1994) have illustrated many of the Australian mitrids.

Fossil mitrids have been found as far back as the Cretaceous. The earliest known Australian fossils are from the Miocene with some genera surviving to Recent times. *Mitra* (*Eumitra*) existed in the Miocene of Australia and New Zealand and became extinct in this region during the Pliocene, but Lozouet (1991) has described Recent species from the Coral Sea and New Caledonia. Another subgenus of *Mitra*, *Dibaphimitra*, was in south-eastern Australia during the Miocene but now is only known from the

Caribbean area. The subgenus *Cancilla* was also in south-eastern Australia during the Miocene and is common in tropical Australia, with one species living on the New South Wales continental shelf.

Family Volutomitridae

Volutomitrids are marine snails with a more or less fusiform shell 4-50 mm in length, and with two to five columellar plaits and a paucispiral, mammillate protoconch. The shell surface is smooth or axially sculptured and the siphonal canal is not notched. The structure of the mid-oesophagus is different from any other neogastropod in that the gland of Leiblein is only partially separated from the mid-oesophagus. The single accessory salivary gland is small and the hypobranchial secretion is colourless. The operculum, when present, is rudimentary and the radula formula is 1-1-1 or 0-1-0.

These snails were initially included in the Mitridae, but were later given subfamilial status in the Volutidae. Cernohorsky (1970) treated the group as a distinct family and revised the world genera. Ponder (1972a) provided anatomical confirmation of the distinctiveness of this group, and additional anatomical studies have been made by Arnaud & Van Mol (1979), and Kantor & Harasewych (1992) who have suggested a relationship with the Cancellariidae.

Shells are variable in outline, although more or less fusiform (Fig. 15.170A, E). The spire is high to low, the protoconch with one to three (usually one and a half to two) smooth, bulbous or dome-shaped whorls. The teleoconch consists of three to eight flat-sided, convex to concave whorls which are either smooth or sculptured with axial ribs, spiral striae, or peripheral nodules and they often have an impressed sutural girdle. The aperture is usually rather narrow, the outer lip smooth or lirate within, and has two to five relatively widely spaced, often irregularly placed columellar plaits. The second posterior columellar plait is larger than the first. The siphonal canal is short or moderately long, without a distinct notch.

The head-foot is variously coloured, usually spotted or marbled, the head short and broad with moderately short and stubby tentacles. Eyes are small to large and situated on the sides of the thickened base of the tentacles. The foot is broad and in the genus *Peculator* has a rudimentary operculum on the dorsal surface of the posterior end (Fig. 15.170E), but other genera lack an operculum. The osphradium is broad and bipectinate, with numerous filaments and the ctenidium has many triangular filaments. The kidney is of the pycnonéphridien type in which the two types of renal lamellae are interdigitated. The nervous system is highly concentrated (Ponder 1972a).

Nothing is known about the feeding habits of Volutomitridae. The radula (Fig. 15.170B) is rachiglossate and has a formula of 1-1-1 (*Volutomitra*) or 0-1-0 (*Microvoluta*). The central tooth is wishbone-shaped and each tooth is equipped with moderately long or short, simple and curved cusps. The laterals, when present, are needle-like and lack cusps. Volutomitrid central teeth are somewhat convergent in shape with those of the volutid genus *Scaphella*, this being one reason for which the family was aligned with volutids. The alimentary canal (Fig. 15.170D) has a short proboscis, with a single accessory salivary gland (Fig. 15.170C). The ducts to the large salivary glands are embedded in the oesophageal wall. There is only a very small gland of Leiblein (Fig. 15.170D) and the long mid-oesophagus has well-developed glandular dorsal folds.

Little information is available on reproduction and life history, but the reproductive systems of a New Zealand species of *Peculator* have been studied (Ponder 1972a). The male system has an open pallial duct and a penial groove, whereas the female system conforms to the normal neogastropod pattern. The egg capsules of *Microvoluta* are hemispherical (Ponder 1972a), however, they are unknown for most of the family. Development is direct in *Microvoluta* (Ponder 1972a) and presumably in other

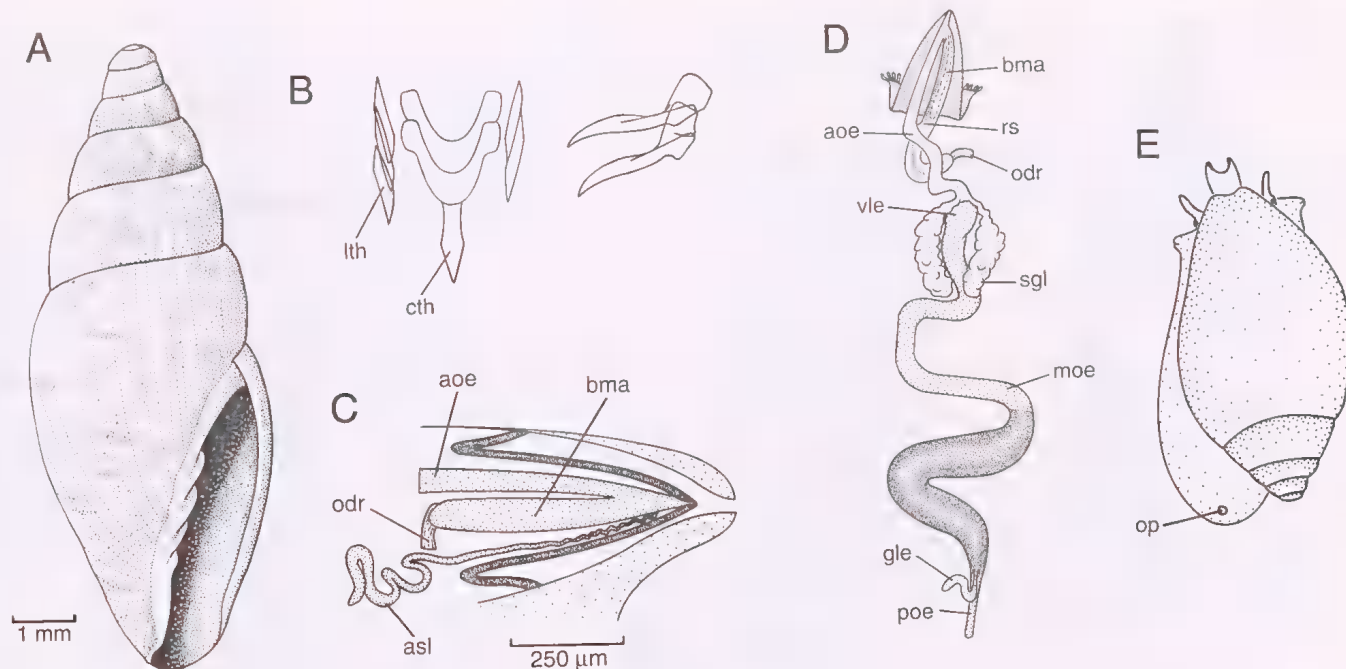


Figure 15.170 Family Volutomitridae. A, *Microvoluta australis*, shell, apertural view. B, two transverse rows of radular teeth of *Volutomitra fragillima*, to the right, a side view of the central teeth. C, the anterior gut of *Microvoluta marginata*, lateral view. D, foregut of *Peculator hedleyi*. E, *Peculator hedleyi*, crawling animal, dorsal view. aoe, anterior oesophagus; asl, accessory salivary gland; bma, buccal mass; cth, central tooth; gle, gland of Leiblein; lth, lateral tooth; moe, mid-oesophagus; odr, odontophoral retractor muscle; op, operculum; poe, posterior oesophagus; rs, radular sac; sgl, salivary gland; vle, valve of Leiblein. (B, after Thiele, from Cernohorsky 1970; C–E, after Ponder 1972a)

living members of the family, judging from protoconch morphology. However, a few fossil species may have had larval development as they have multi-whorled protoconchs (Cernohorsky 1970).

Volutomitrids inhabit cool seas of both hemispheres living in mud and sand in water depths of 10–1900 m, at water temperatures ranging from -1°C to $+12^{\circ}\text{C}$. Only '*Waimatea*' *obscura* occurs intertidally at higher temperatures (up to 20°C) in Australia and New Zealand (Cernohorsky 1970).

Cernohorsky (1970) recognises six genera in this family, all of which occur in the Australasian region. There is one endemic Australasian genus, *Peculator*, which has Recent species. Maxwell (1992) synonymised *Waimatea*, based on a fossil New Zealand species, with *Volutomitra*, but the generic position of the living Australasian '*W.*' *obscura* is uncertain (P. Maxwell personal communication). *Proximitra* is a fossil genus which was endemic to New Zealand and Australia, but other fossil species have been found in Europe and the United States of America. Species of *Volutomitra* are not known from Australia (there are several species in New Zealand), and most of the known species are from the Northern Hemisphere. *Conomitra* is a fossil genus with a Northern Hemisphere distribution but one species is known from Australia and one from New Zealand. *Microvoluta* (Fig. 15.170A) is represented largely by fossil and Recent species from Australia and New Zealand, but is also found in the Caribbean, the Philippines and South Africa.

The earliest fossils of this family are from the Upper Cretaceous of Europe and the United States of America. The earliest known New Zealand volutomitrids are from the Eocene, but the family is not known until the Miocene in Australia.

Family Costellariidae

The shells of these marine snails range from 3–80 mm in length and are fusiform to ovate, closely resembling those of the Mitridae, although differing in having predominantly axial sculpture. Shells have three to six columellar plaits, and the foot lacks an operculum. Features that distinguish this family from the conchologically similar mitrids include the anterior gut having

paired accessory salivary glands and a gland of Leiblein, the radula with broad, multicuspidate central teeth and unicuspidate lateral teeth, and the hypobranchial secretion being yellow-green.

This family was given subfamily (as Vexillinae) rank in the Mitridae by Thiele (1929–1935) until Azuma, in 1965, raised the Vexillinae to family rank based on radular characters. Risbec (1955) noted that the anterior alimentary canal is very different from that of Mitridae, and this was supported by Ponder's (1972a) study of the anatomy of three families with similar 'mitriform' shells (Mitridae, Vexillidae, and Volutomitridae); Ponder defined each of these groups as separate families using anatomical characters. Maes & Ræihle (1975) have described in detail the biology and anatomy of an American species, *Thala floridana*. Cernohorsky (1970) reviewed the genera in the family and (1976) demonstrated that the earlier family name Costellariidae should be used. He also (Cernohorsky 1980) revised the New Zealand and temperate Australian fossil and Recent species of *Vexillum* and *Austromitra*. A species level review was provided by Pechar *et al.* (1980) and Wilson (1994) has illustrated most of the Australian species.

The shell is more or less fusiform, slender or ovate, with distinct sutures (Fig. 15.171A–C). Sculpture is predominantly axial, rarely absent, with ribs, beads, grooves or weak spiral ridges. The aperture is rather narrow, the outer lip always lirate within, except in the Cretaceous genus *Mesorhytis* and some species of *Austromitra*. The inner lip has three to six well-developed columellar plaits, the posteriormost plait being larger than the second, and often having a callus pad on the parietal wall. The short, notched siphonal canal is straight or recurved.

The foot is multicoloured and markedly expanded, the head bears long, slender tentacles and a moderately long anterior siphon extends beyond the anterior canal. The osphradium is large, bipectinate and lies on the left alongside the ctenidium which has triangular filaments.

Species in this family are carnivorous, some being known to feed on other molluscs and on tunicates, although there is little information about their diets. The New Zealand *Austromitra rubiginosa* feeds on various species of tunicates and embeds its

15. PROSOBRANCHS

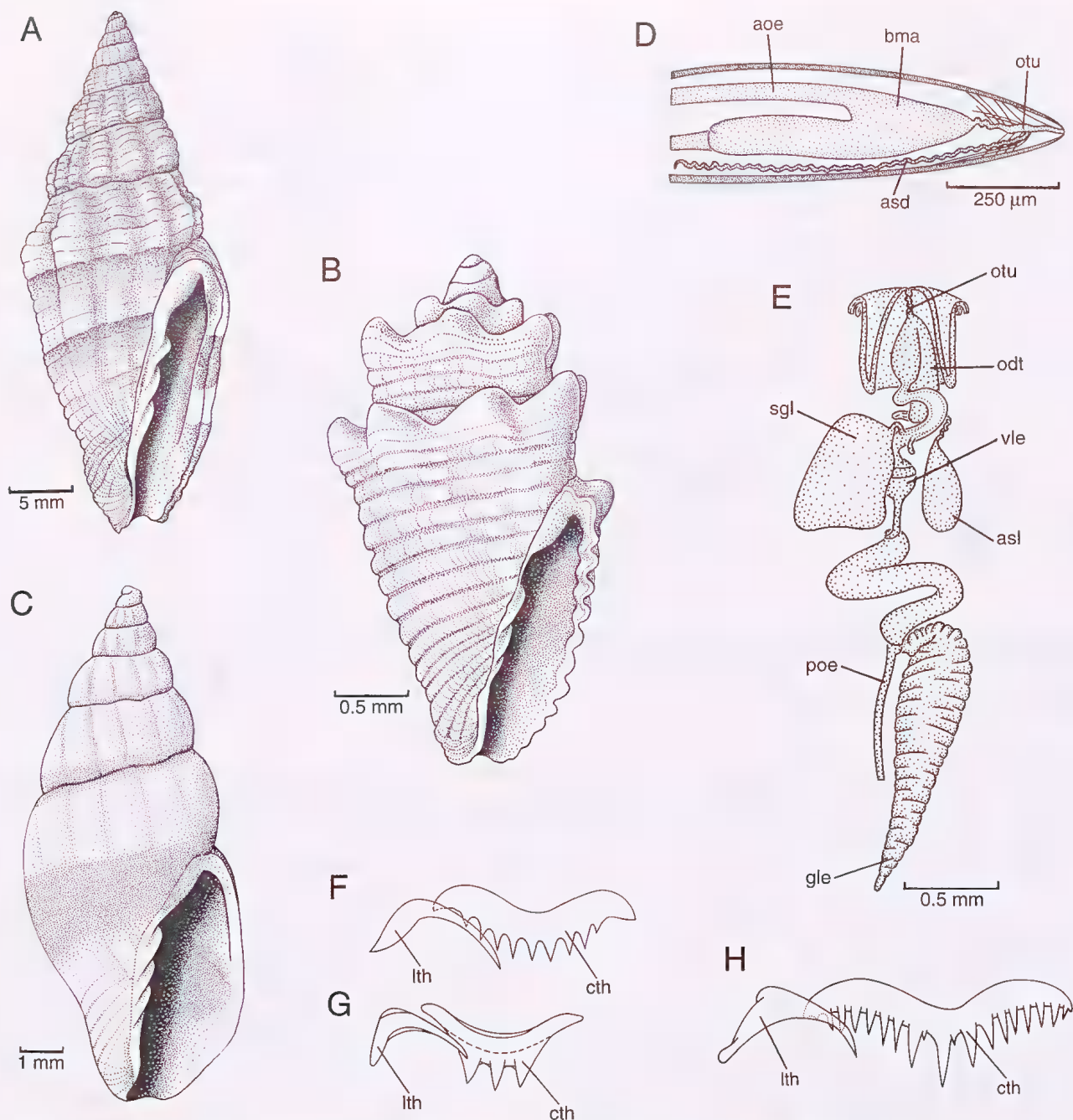


Figure 15.171 Family Costellariidae. A–C, shells, apertural views: A, *Vexillum rugosum*; B, *Vexillum (Pusia) bernhardina*; C, *Austromitra analogica*. D, *Vexillum plicarium*, the anterior gut, lateral view. E, *Austromitra rubiginosa*, the anterior part of digestive system, dorsal view, with the right salivary gland removed. F–H, radular teeth, central tooth with one of the lateral teeth: F, *Vexillum (Pusia) luculentum*; G, *Vexillum (Pusia) patriarchalis*; H, *Vexillum (Vexillum) rugosum*. aoe, anterior oesophagus; asd, accessory salivary gland duct; asl, accessory salivary gland; bma, buccal mass; cth, central tooth; gle, gland of Leiblein; lth, lateral tooth; odt, odontophore; otu, oral tube; poe, posterior oesophagus; sgl, salivary gland; vle, valve of Leiblein. (D, E, after Ponder 1972a; F–H, after Cernohorsky 1970) [A–C, S. Weidland; D–H, C. Eadie]

eggs in their tests (Ponder 1972a). The genus *Thala*, which does not occur in Australia, has been shown to produce a quick-acting poison (probably secreted from the accessory salivary glands) that it uses to kill other molluscs – it then feeds on selected tissue deep in the body of the prey (Maes & Raeihle 1975). It is possible that other costellariids feed in a similar manner. Some *Vexillum* species envelop their prey with the foot.

The radula of the Costellariidae differs from the Mitridae in having a slightly curved, broad central tooth with three to many small cusps on the cutting edge and a sickle-shaped lateral tooth on each side of it (Fig. 15.171F–H). Costellariids also differ from mitrids in having accessory salivary glands and a gland of Leiblein (Fig. 15.171E), and in lacking an epiproboscis, a posterior caecum on the stomach and a peristomal rim on the mouth (Fig. 15.171D). The costellariid hypobranchial secretion is predominantly yellow-green rather than purple as in mitrids. The kidney is of the pycnonéphridien type, having the primary and secondary lamellae interdigitated.

Larvae develop directly or through a free-living veliger stage. Egg capsules of *Austromitra* are inverted-hemispherical (Ponder 1972a), but hemispherical in the American *Thala* (Maes & Raeihle 1975). The juveniles, upon emergence, have no operculum. The reproductive structures of costellariids are very similar to those of Mitridae.

Costellariids are primarily sand dwellers, but some inhabit coral reefs living beneath rocks and coral boulders. They live in shallow to deep water in temperate to tropical seas but are not known to live below about 930 m. Species of *Vexillum (Pusia)* (Fig. 15.171B) inhabit cracks and crevices of coral reefs and the underside of stones, but members of the typical subgenus *Vexillum* (Fig. 15.171A) and *V. (Costellaria)* live buried in mud and sand.

According to the most recent revisions (Cernohorsky 1970, 1980), this family contains four Recent genera, two of which occur in Australia (*Vexillum* and *Austromitra*). All three subgenera of *Vexillum* (*Vexillum sensu stricto*, *Costellaria* and *Pusia*) occur in

Australia. Species of the Australian and New Zealand genus *Austromitra* (Fig. 15.171C) – as recognised by Cernohorsky (1980) – are highly variable both in colour and sculpture. They generally have unicoloured or banded shells and in comparison with species of *Vexillum* have a less conical and more papillose protoconch, and lack the prominent parietal callus pad.

Austromitra first appeared in Australia during the Upper Eocene and is the oldest known fossil Australian costellariid. It is found later in New Zealand, first appearing in the Upper Miocene. There are also late Tertiary fossils attributed to this genus from Patagonia (Argentina) and South Africa. Living species are confined to Australia, New Zealand and South Africa. In all, Cernohorsky (1980) recognised 14 fossil Australasian species, nine from Australia and five from New Zealand. There are four Recent species in *Vexillum* (*Costellaria*) in temperate Australia, where it is first recorded from the Mid-Miocene. The genus *Mesorhytis*, which became extinct during the Palaeocene, is believed to be the oldest costellariid (Cernohorsky 1970) and ranges back to the Cretaceous.

Superfamily CANCELLARIOIDEA

Most current workers (Taylor, J.D., Morris & Taylor 1980; Boss 1982; Ponder & Warén 1988; Petit & Harasewych 1990) follow Ponder (1973) in regarding Cancellarioidea (synonym Nematoglossa) as a superfamily within the Neogastropoda, distinguished by a unique anterior alimentary system, yet resembling neogastropods in other respects. More recently, however, Kantor & Harasewych (1992) reported similar modifications in the anterior alimentary system of the muricoidean family Volutomitridae and suggested that a re-assessment of the taxonomic rank and systematic position of Cancellarioidea may be

in order. A phylogenetic analysis of several higher level molluscan taxa by Rosenberg, Kuncio, Davis & Harasewych (1994) and based on 28S rRNA sequence data indicated that Cancellariidae originated within the Muricoidea.

The Cancellarioidea includes the Cancellariidae, which extends from the Upper Cretaceous to the present, and the Paladmetidae, known only from the Upper Cretaceous and assigned to the Cancellarioidea on the basis of putative superficial conchological similarity. Ponder & Warén (1988) listed Paladmetidae as a synonym of the cancellariid subfamily Admetinae.

Family Cancellariidae

Members of the marine family Cancellariidae are characterised by small to medium-sized, fusiform to ovate, gradate to scalariform, dextral shells (Fig. 15.172A–D), usually with axial and spiral sculpture producing a cancellate or reticulate surface from which the family derives its name. Most species have two to three distinctive columellar folds or plaits that, at regular intervals (usually 120 to 270°), become expanded in apposition to correspondingly enlarged apertural teeth to form 'internal varices' that reinforce the shell from within, yet are difficult to discern externally. Until recently, the family has been divided, largely on the basis of shell characters, into three subfamilies: Admetinae, characterised by smaller, thinner shells lacking an umbilicus and columellar folds; Cancellariinae, characterised by heavy shells with reticulate or cancellate sculpture and three columellar folds, but lacking an umbilicus or external varices; Trigonostominae, characterised by high spired, strongly to weakly shouldered, umbilicate to pseudo-umbilicate shells, usually with two columellar folds and weak varices. Taxa included in the Trigonostominae are now generally regarded as comprising a

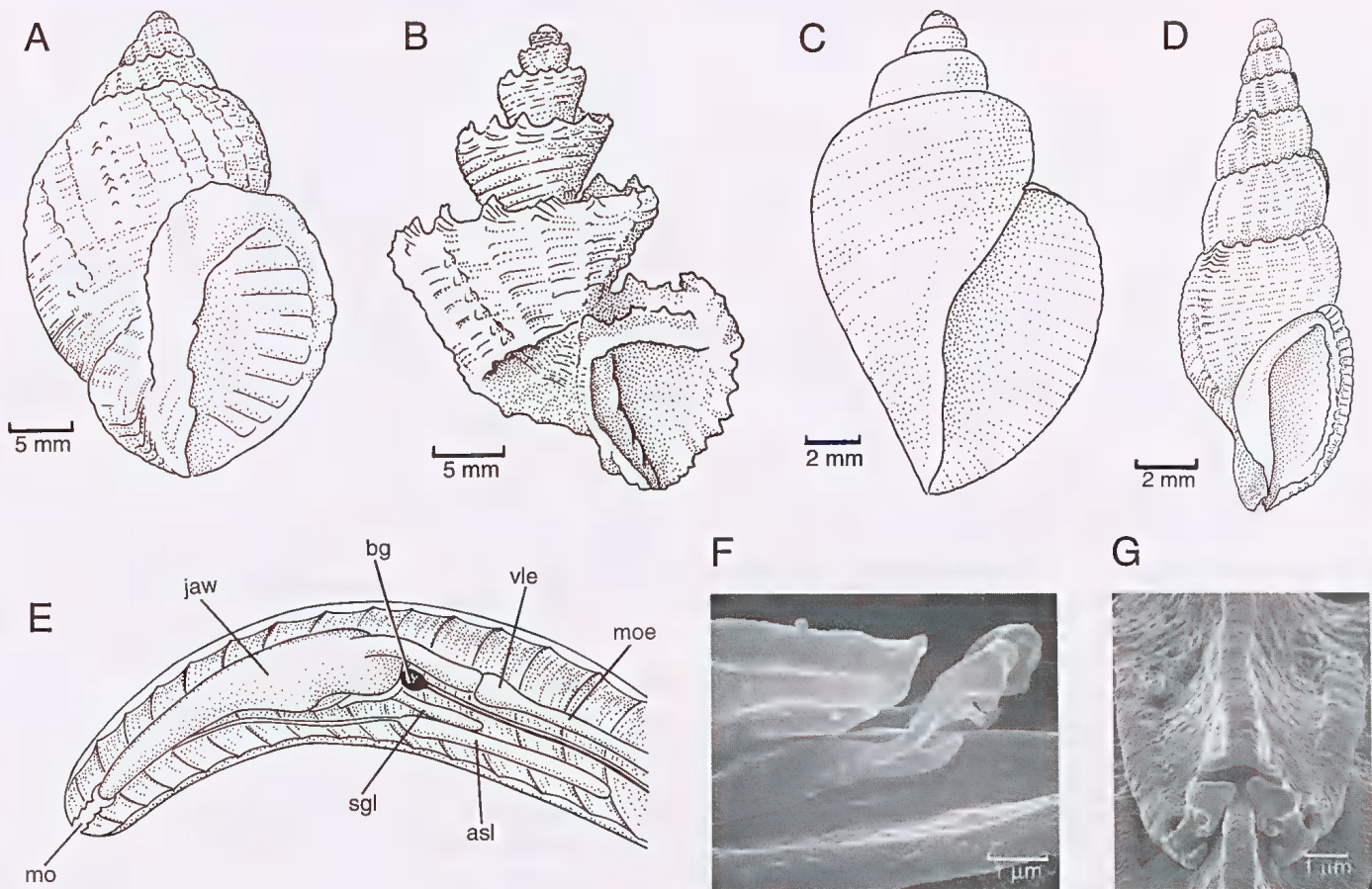


Figure 15.172 Family Cancellariidae. A–D, shells of Australian representatives of the four subfamilies, apertural view: A, Cancellariinae, *Cancellaria elegans*, found along the coasts of Queensland and New South Wales; B, Trigonostominae, *Trigonostoma scalare*, found from the central coast of Western Australia to southern Queensland; C, Admetinae, *Zeadmete kulanda*, found off New South Wales in waters ranging from 800 to 900 m in depth; D, Plesiotritoninae, *Tritonoharpa ponderi*, found off southern Queensland-northern New South Wales; E, *Trigonostoma scalare*, anterior half of the proboscis, lateral view, the left wall removed to display the cancellarioid features of the anterior alimentary system; F, G, *Trigonostoma scalare*, distal tip of radular tooth: F, lateral view; G, frontal view. asl, accessory salivary gland; bg, buccal ganglion; jaw, jaw; mo, mouth; moe, mid-oesophagus; sgl, salivary gland; vle, valve of Leiblein. [A–E, M. Ryan; F, G, M.G. Harasewych]

15. PROSOBRANCHS

grade rather than a clade, resulting in this subfamily being considered a synonym of Cancellariinae by most recent workers (Ponder & Warén 1988; Wilson 1994). More recently, Beu & Maxwell (1987) erected the subfamily Plesiotritoninae to include very high-spired varicose cancellariids with non-collabral axial sculpture that were previously placed in the families Buccinidae, Fascioliidae and Ranellidae. Petit & Harasewych (1990) listed over 1800 species-level taxa in the Cancellarioidea. The Australian Cancellariidae were revised by Garrard (1975), who discussed and figured 38 species distributed among 12 genera and subgenera. Beu & Maxwell (1987) included an additional seven Recent species in two genera from Australia. Forty-six extant species distributed among 14 genera are discussed and well illustrated by Wilson (1994).

The principal diagnostic feature of the family is the modified anterior alimentary system (Fig. 15.172E) that includes: a radular ribbon comprising a single row of very long, narrow, ribbon-like teeth (Fig. 15.172F, G), generally with a complex arrangement of interlocking cusps at their anterior ends (Petit & Harasewych 1986); a large chitinous jaw that is tubular anteriorly and expanded posteriorly to surround the buccal mass; a greatly shortened anterior oesophagus (with the valve of Leiblein near the rear of the buccal mass) situated at the anterior end of a long proboscis; and a greatly simplified, alimentary system posterior to the valve of Leiblein. The majority of admetine species lack a radula, but have the other features listed.

Graham (1966) and Olsson (1970) conjectured that cancellariids feed on soft-bodied micro-organisms, whereas Harasewych & Petit (1982, 1984, 1986) have suggested that modifications of the anterior alimentary system are adaptations for suctorial feeding. O'Sullivan, McConnaughey & Huber (1987) documented the diet and feeding behaviour of *Cancellaria cooperi*, a Californian species that feeds by sucking the blood of rays and sharks. Loch (1987b) reviewed reports of Australian cancellariids feeding on bivalves and sand-dwelling gastropods.

The animals are light tan in colour, often with reddish brown spots covering the tentacles, proboscis, mantle edge and the dorsal and lateral portions of the foot. Some members of the Cancellariinae have a left cephalic tentacle that is bifurcated or modified to some degree (Harasewych & Petit 1982). Cancellariids are similar to other neogastropods in the morphology of the head foot, pallial complex, reproductive and excretory systems. The nervous system differs from that of other neogastropods chiefly in the extreme anterior location of the buccal ganglia and the resultant elongation of the cerebro-buccal connectives. Details of the anatomy of representative members of two of the three subfamilies have been published and compared by Harasewych & Petit (1982, 1984, 1986).

The spatulate egg capsules of cancellariids resemble those of most neogastropods in consisting of leathery lenticular capsules with a dorsal pre-formed hatching aperture, supported on a narrow stalk that is very long in sand-dwelling species and shorter or absent in species that live on hard substrata. The number of ova per capsule (five to 5000 ova) and mode of development (direct lecithotrophic-planktotrophic) vary with species and are reviewed by Pawlik, O'Sullivan & Harasewych (1988) and Knudsen (1992). Opercula are present in larvae, but absent in adults.

The family contains over one hundred nominal genus-level taxa (Petit & Harasewych 1990), 14 of which occur in Australia. The subfamily Admetinae, which has a predominantly polar distribution, is represented in the Australian fauna by a single, bathyal species, *Zeadmete kulanda*, with congeners in New Zealand. Two genera of the subfamily Plesiotritoninae occur in Australia, the predominantly east African *Africotriton*, with a single bathyal species reported from off New South Wales, and the circumtropical *Tritonoharpa* with seven species distributed through the shallow tropical regions. The remaining Australian species and genera are referable to the subfamily Cancellariinae. Of the 14 species of *Trigonostoma*, only one inhabits the temperate waters off South Australia, the others are tropical. All inhabit the continental shelf at varying depths. Species of the

shallow water genus *Cancellaria sensu lato* are divided among the tropical subgenus *C. (Merica)* (two species) and the primarily temperate subgenera *C. (Nevia)* (one species) and *C. (Sydaphera)* (seven species). Also present in Australian waters are the tropical neritic genera *Fusiaphera* and *Admetula*, the endemic genus *Pepta*, and the bathyal genera *Bonellitia*, *Gergovia*, *Inglisella* and *Vercomaris*, which, based on limited data, appear to be restricted to Australian waters.

Cancellariids are well represented in the Australian Tertiary; some two dozen species have been documented by Tate (1889), Darragh (1970) and Beu & Maxwell (1987).

Superfamily CONOIDEA

The Conoidea (formerly known as Toxoglossa) is a large and diverse superfamily traditionally regarded as comprising three extant families, Turridae, Conidae and Terebridae. The Turridae occur worldwide, and are the most widely distributed of these families. There are probably more than 4000 living turrid species, of which about 10% probably occur in Australia (Wells 1991a). The Conidae include about 500 living species, primarily tropical and almost all usually placed in *Conus*; about 100 occur in Australia. Terebridae are the smallest family, with about 150 extant species, also primarily tropical; more than one-third of the species occur in Australia. A recent revised classification of the superfamily, based partly on a cladistic analysis, raised three traditional turrid subfamilies to family rank and transferred several others to the Conidae (Taylor, J.D., Kantor & Sysoev 1993). However, the taxonomy of the superfamily remains poorly resolved. For example, Turridae is both diphyletic and paraphyletic in the treatment of J.D. Taylor *et al.* (1993), and genus- and species-level classifications also remain problematic. Thus, the traditional arrangement is used here.

Members of the Conoidea inhabit an extremely broad range of marine environments, from the intertidal zone to abyssal depths in all the world's oceans. The group is included here in the Neogastropoda, together with the superfamilies Muricoidea and Cancellarioidea, following Ponder (1973), J.D. Taylor & Morris (1988) and Ponder & Warén (1988).

The Conoidea differs from the other neogastropod superfamilies in having the proboscis formed by an anterior elongation of the buccal tube with the buccal mass located at its base, a permanent rhynchodeum or proboscis sheath, a venom apparatus consisting of an unpaired bulb and tubular secretory duct opening into the buccal cavity (Fig. 15.173), and the radula probably consisting primitively of rows of five teeth. The radula has tended to lose the central and lateral teeth, and to develop large, complex, toxoglossate marginal teeth, specialised for hypodermic venom injection (Taylor, J.D. & Morris 1988; Taylor, J.D. *et al.* 1993).

Shell shape differs markedly among the three families. In the Turridae, the shell is usually spindle-shaped and has a large last whorl, often with a siphonal canal. In the Conidae, the shell is obconic or biconic with a very large last whorl, usually a short spire, and a long, narrow aperture without a distinct siphonal canal. In the Terebridae, the shell has a very elongate spire and a relatively small last whorl with a siphonal notch, but the siphonal canal is absent or very short. Throughout the superfamily the shell usually has a distinct posterior sinus that accommodates the exhalant region of the mantle.

The head in the Conoidea consists of a tubular rhynchodeum (Fig. 15.173) or proboscis sheath – referred to as a proboscis sac by Fretter & Graham (1962) and as a labial tube by B.A. Miller (1975, 1979). Its opening is the rhynchostome (Fig. 15.173) or false mouth. The head bears a pair of tentacles with subterminal eyes, but tentacles are absent in some terebrids. The foot is usually small, short and broad in the Terebridae, long and narrow in the Conidae, and of variable form in the Turridae. It bears an operculum that is often much smaller than the shell aperture, especially in conids. As in most neogastropods there is a transverse anterior pedal gland, and, in female conids but not in turrids (Fretter & Graham 1962;

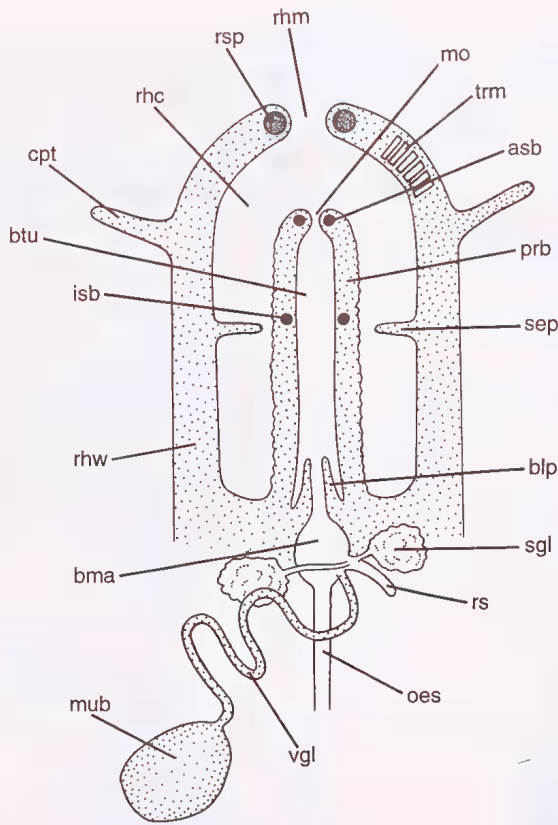


Figure 15.173 Superfamily Conoidea. Composite diagrammatic frontal section of the structures associated with feeding in a generalised conoidean gastropod. asb, anterior sphincter of buccal tube; blp, buccal lips; bma, buccal mass; btu, buccal tube; cpt, cephalic tentacle; isb, intermediate sphincter of buccal tube; mo, mouth; mub, muscular bulb of venom apparatus; oes, oesophagus; prb, proboscis; rbc, rhynchocoel; rhm, rhynchostome; rhw, rhynchodeal wall; rs, radular sac; rsp, rhynchostomal sphincter; sep, septum; sgl, salivary gland; trm, transverse muscles of rhynchodeal wall (shown in part only); vgl, venom gland. (After Taylor, J.D. *et al.* 1993) [C. Eadie]

Smith, E.H. 1967a), a ventral pedal gland that appears to toughen and mould the outer coat of the egg capsule. The mantle cavity is typical of the order, and it contains a prominent bipectinate osphradium, the major olfactory receptor. The inhalant siphon is longest in those turrids with a long siphonal canal on the shell. In the Conidae (Pl. 29.5) and Terebridae, it may extend well beyond the shell.

Most conoidean proboscides differ markedly from the proboscides of other neogastropod superfamilies in being formed by an elongation of the buccal tube (Figs 15.173, 5.175A–C) or by elongation and modification of the rhynchodeal walls (Taylor, J.D. & Morris 1988), rather than from the oesophagus. The typical conoidean buccal mass is at the base of the proboscis and does not move when the proboscis extends and contracts. Ponder (1973), J.D. Taylor & Morris (1988) and J.D. Taylor *et al.* (1993) reviewed the diversity of proboscis types in the superfamily.

All members of the Conoidea are probably predatory, and most have a rapid-strike, chemically aided system that paralyses prey. The presence of prey is determined at a distance by chemoreception, but contact chemoreception is usually necessary to elicit the complete sequence of feeding activity.

The principal feeding organ, the radula, is variously specialised. In many species in the Turridae, as in the other two families, each radular tooth row contains only one pair of marginal teeth. The putatively more primitive turrids have three, four or five teeth per row, and their marginal teeth are relatively unmodified. In Conoidea with marginal teeth only, these are hypertrophied and highly modified into tubular harpoon- or hypodermic needle-like structures (see Fig. 1.14E; Kantor 1990a; Taylor, J.D. *et al.* 1993) that simultaneously impale the prey and convey neurotoxic venom from the buccal cavity via the proboscis into the wound. The

paralysed prey is then drawn into the proboscis sheath and swallowed whole. The venom apparatus comprises an unpaired muscular bulb and tubular gland (Fig. 15.173) that enters the buccal cavity and is probably derived from the unpaired oesophageal gland (Ponder 1973). The chemical nature of the venom is known only for conids; the active components are small peptides (Olivera, Gray, Zeikus, McIntosh, Varga *et al.* 1985; Olivera, Rivier, Clark, Ramilo, Corpuz *et al.* 1990).

Salivary glands vary considerably among conoidean gastropods. They are either paired or unpaired, the ducts enter either the buccal mass or the radular sac, and they may be accompanied by or replaced by tubular accessory salivary glands. In turrids, they are typically paired, but one is often larger, and the ducts enter the buccal mass (Smith, E.H. 1967a; Shimek 1975). At least one turrid species lacks salivary glands (Smith, E.H. 1967a). In most conids, the single salivary gland probably results from the fusion of paired glands, as two ducts lead from it, usually entering the radular sac (Bergh 1895; Shaw 1914). A few *Conus* species have long, tubular, paired accessory salivary glands, short ducts of which enter the buccal mass. Schultz (1983) studied their fine structure in two Australian species, *C. flavidus* and *C. vexillum*. The latter species apparently lacks the typical salivary glands. *Conus anemone* is reported to have both types (Bergh 1895 – as *C. maculosus*).

The stomach in Conoidea is not noticeably demarcated from the oesophagus and intestine. As in most carnivorous neogastropods, the stomach is not divided into specialised regions and lacks sorting areas, crystalline style and gastric shield. The stomach forms the base of a 'U' in the visceral mass between oesophagus and intestine, and is the site of entry of the ducts from the digestive glands (Smith, E.H. 1967b; Ponder 1973).

The conoidean kidney is divided into separate primary and secondary parts, in contrast to those of the Muricoidea in which these parts interdigitate (Ponder 1973). As is typical of neogastropods, the sexes are separate and fertilisation is internal. Egg capsules of turrids are typically lens- or dome-shaped and have the flat lower side cemented to the substratum (Shimek 1983a; Bouchet 1990), those of conids are flask-shaped and are attached to the substratum by a basal plate (Pl. 29.4; Kohn & Perron 1994), and those of the one species of Terebridae known are oblong and are attached to sand grains by thin threads (Miller, B.A. 1975).

The Conoidea occurs throughout the world oceans, but the biogeographic patterns of the families differ. The Turridae occur in all seas, whereas the Conidae and Terebridae are primarily tropical, but have a few temperate species. All three families are widely distributed along the Australian coasts. Wilson (1994) has described and illustrated many of the species from Australian waters.

The earliest conoidean fossils are recorded from the mid-Cretaceous (Powell 1966). The Turridae are the oldest family. The Conidae and Terebridae probably originated early in the Tertiary. In Australia, the oldest fossil turrids are Eocene and the oldest conids and terebrids are Late Oligocene to Early Miocene (Darragh 1985).

Family Turridae

The family Turridae occurs worldwide and is highly diverse from polar seas to the equator and from shallow subtidal to abyssal depths. It is the largest mollusc family and includes more than 600 described genera and more than 10 000 described Recent and fossil species in about 17 subfamilies (Bouchet 1990); of these perhaps 4000 are valid extant species (Wells 1991a). J.D. Taylor *et al.* (1993) reclassified the Turridae at the subfamily level, based in part on a cladistic analysis. Powell summarised the genus-level taxonomy and geographic distribution of the family (1966) and monographed the Indo-Pacific members of the large subfamilies Turrinae and Turriculinae (1964, 1969). Kilburn (1983–1995) continues to monograph the Turridae of southern Africa and Mozambique in a series of publications with broader geographic application.

15. PROSOBRANCHS

The diverse Australian turrid fauna certainly comprises more than 400 species. Hedley, in 1922, reviewed all the then known Australian species and reported about 370 species. Wells (1990, 1991a, 1991b) revised the Australian species of the genera *Splendrillia*, *Austrodrillia*, *Clavus*, *Plagiostropha*, *Tylotiella*, *Inquisitor* and *Ptychobela*. In other accounts, Laseron (1954c) reported 142 species from New South Wales; Cotton (1952) reported 110 species from South Australia; Macpherson & Gabriel (1962) reported 97 species from Victoria; May (1921) reported 55 species from Tasmania; and Wells (1990, 1991a, 1991b) and Wells & Bryce (1988) recorded 21 species from Western Australia. The northern Australian warm-water fauna includes many widely distributed genera and species typical of the Indo-West Pacific such as *Lophiotoma indica* (Fig. 15.174A, B) and *Eucithara coronata* (Fig. 15.174F). The southern Australian fauna by contrast includes taxa that are endemic to this region, such as *Daphnella botanica* (Fig. 15.174C).

One of the main shell characters of the family is the turrid notch or sinus, varying from an obscure concavity to a deep slit on the outer lip, posteriorly on the aperture (Powell 1966). Turrid shells

range in length 1–160 mm (Boss 1982). The shell is typically fusiform but varies widely in spire height, aperture shape, and extent of anterior siphonal canal (Fig. 15.174B–F). Shell sculpture is quite variable, with alternate spiral ridges and grooves and axial nodules usually predominant; a few species have smooth shells. The columella is usually smooth, but has one or more plaits in some species of Borsoniinae, for example in *Bathytoma attractoides*. Some species have lirae or denticles on the inner or outer lip, for example *Etrema curtisiana* and *Eucithara* species. (Fig. 15.174F). A small 'stromboid' notch is present on the lower part of the outer lip in some species, for example species of *Inquisitor*.

The protoconch is often characteristic of genera or species. It may be paucispiral or multispiral and ranges from smooth to elaborately sculptured (Fig. 15.174G; Powell 1966; Bouchet 1990). Powell (1942, 1966) illustrates the range of protoconch form and sculpture in the Turridae.

The shell colour patterns of turrids are usually yellow to dark brown, monochromatic, and spirally arranged (illustrations in Powell 1964).

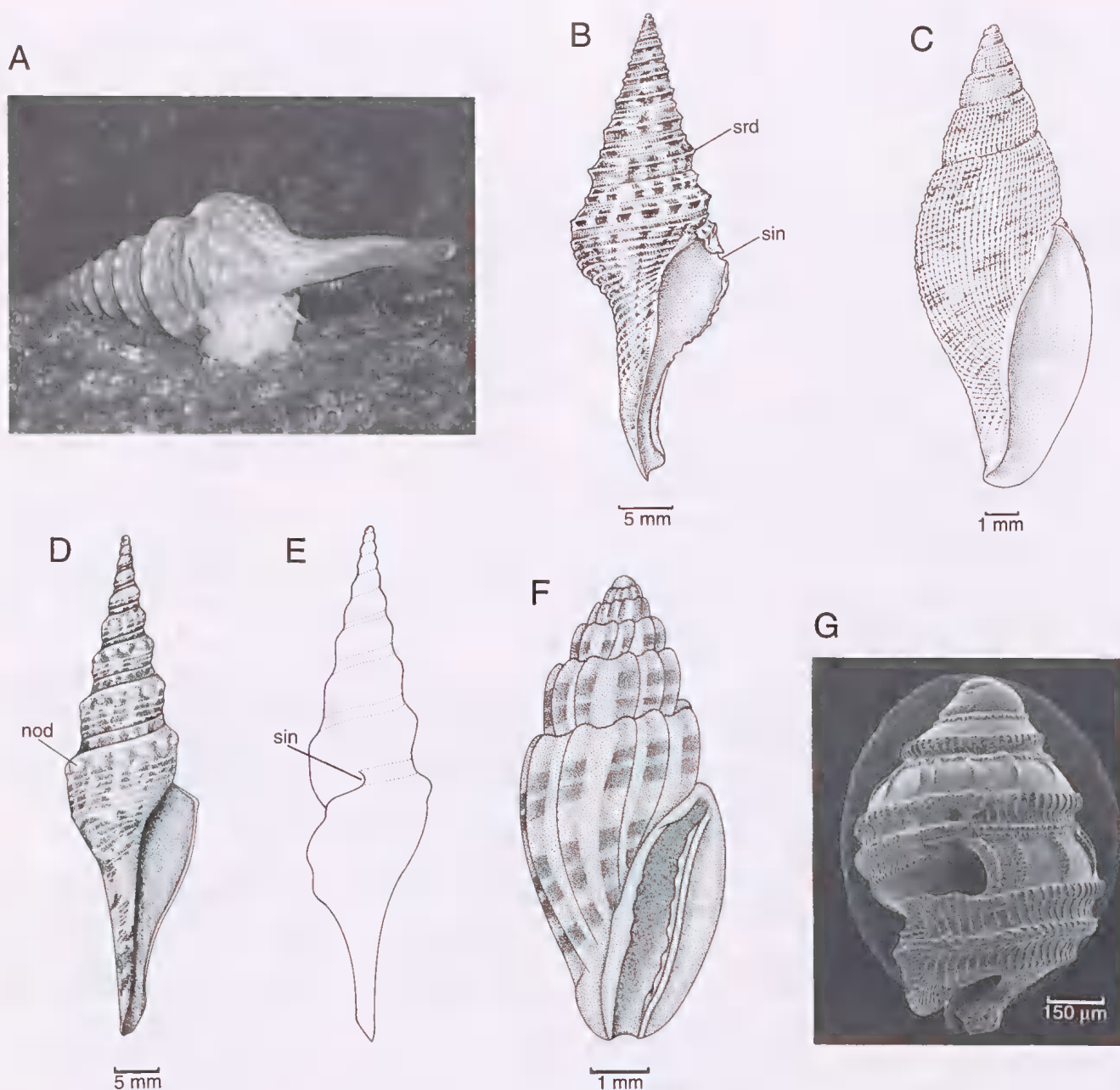


Figure 15.174 Family Turridae. A, *Lophiotoma indica* (Turridae), live specimen showing the sinus above the posterior portion of the foot, the head with tentacles and eyes, and the siphon. B–F, shells: B, *Lophiotoma indica*, apertural view; C, *Daphnella botanica* (Daphnellinae), apertural view; D, E, *Leucosyrinx queenslandica* (Cochlespirinae), apertural and lateral views; F, *Eucithara coronata* (Mangeliinae), apertural view. G, *Carinapex minutissima* (Crassispirinae), elaborately sculptured veliger shell which will become the protoconch of the adult shell. nod, axial nodule; sin, sinus; srd, spiral ridge.

[A, A. Kohn; B, C, R. Plant; D–F, C. Eadie; G, courtesy of C.S. Hickman]

Turrid morphology is summarised above under Conoidea. Important anatomical papers include those of Robinson (1960), E.H. Smith (1967a, 1967b), Sheridan, Van Mol & Bouillon (1973), Shimek (1975) and J.D. Taylor (1985). Of the three families in the superfamily, the Turridae have by far the greatest diversity of proboscides and radulae (Fig. 15.175A–I; Powell 1966; Smith, E.H. 1967a; Kantor 1990a; Taylor, J.D. *et al.* 1993). Extant members of the family conserve a remarkable number of apparently intermediate stages in the evolution of the true toxoglossan radula from the hypothesised rhipidoglossan or taenioglossan ancestor (Shimek & Kohn 1981). In the putatively most primitive subfamilies, the radular membrane is well developed and functional and there are five (Drilliinae) or three (Turriinae and Pseudomelatominae) teeth per row (Fig. 15.175D; McLean 1971). In one of several intermediate configurations the radular membrane is functional but there are only two solid, blade-like teeth per row (Strictispirinae; Fig. 15.175F, G). In the most specialised, especially in toxoglossan subfamilies (for example, Mangeliinae and Borsoniinae), each tooth row contains only two large, elaborate, hollow, harpoon-like marginal

teeth (Fig. 15.175C, H), and the detachable radular membrane functions only in transporting teeth into a storage region of the radular sac (Shimek 1975).

Development has been studied only in a few Northern Hemisphere species and is best known in *Oenopota levidensis* (Shimek 1986). Lens-shaped egg capsules (illustrations in Powell 1964; Shimek 1983a) contain 20 to 250 eggs. Those of *Oenopota* species hatched as free-swimming veligers after 50 days. The veligers fed and grew in the plankton for about a week, then became demersal and continued larval development for about four more weeks before metamorphosing (Shimek 1986). Shuto (1983) illustrated protoconchs of numerous Australian turrid species.

Turrids inhabit a wide array of marine benthic environments, from shallow subtidal to abyssal depths. Most occupy soft substrata. Patterns of diversity are poorly known; however, it appears probable that the highest diversity occurs at bathyal depths (Bouchet & Warén 1980).

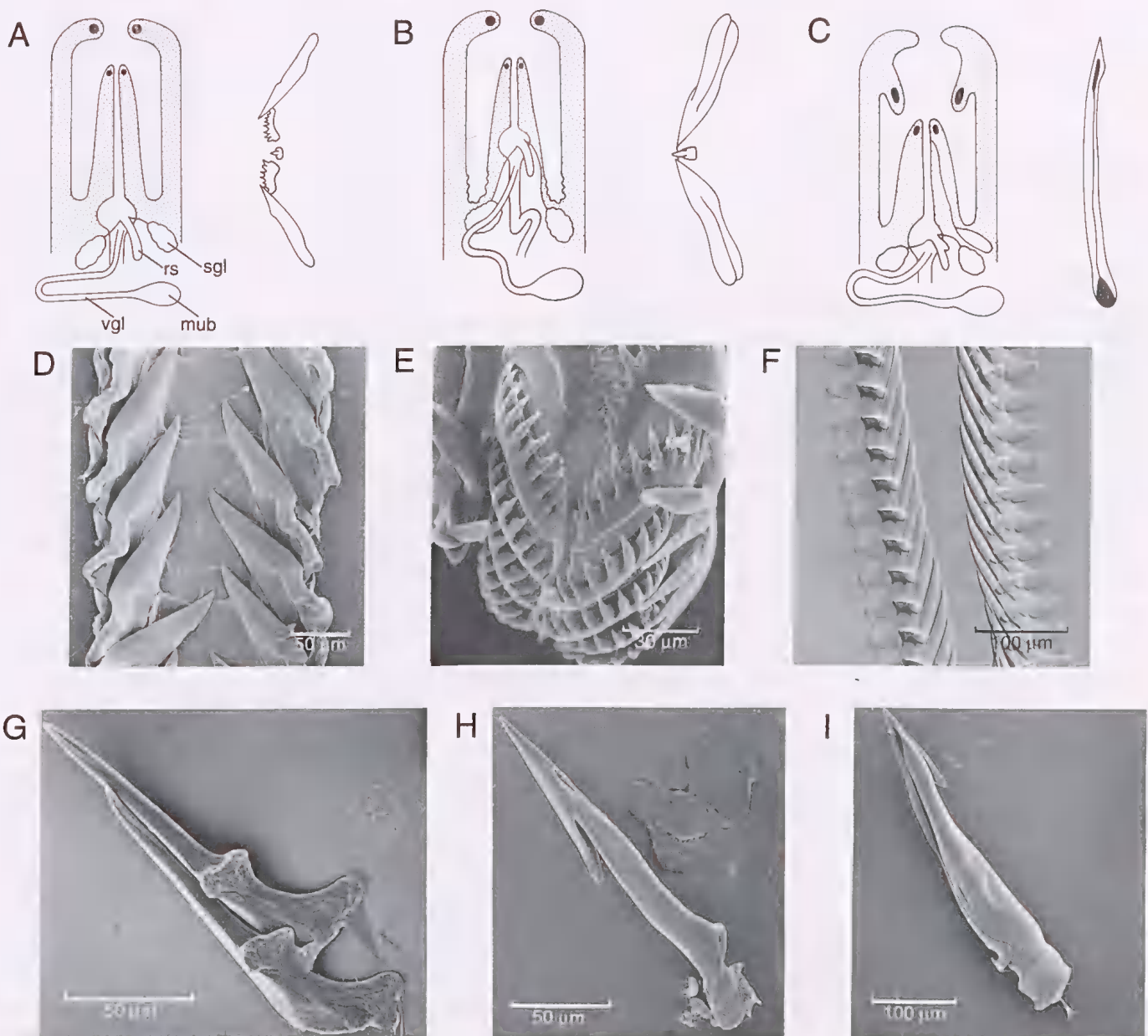


Figure 15.175 Family Turridae. A–C, diagrammatic frontal sections of three types of foregut morphology and the radula type associated with each: A, *Clavus unizonalis* (Drilliinae), radula with five teeth per row; B, *Clionella sinuata* (Clavatulinae), radula with three teeth per row; C, *Ophiodermella inermis* (Borsoniinae), radula with two hollow, harpoon-like teeth per row, only one of which is shown. D–I, portions of radulae: D, *Gemmula deshayesii* (Turriinae), each tooth row comprises a large central tooth and a pair of wishbone-shaped marginal teeth – a strong radular membrane is present; E, *Calliclava albolaqueata* (Drilliinae), several radular tooth rows showing the small central teeth, large, prominently denticulate lateral teeth and blade-like marginal teeth – a strong radular membrane is present; F, G, *Strictispira paxilla* (Strictispirinae), radula tooth rows *in situ* on radular membrane (F) showing the paired, solid marginal teeth with blade and large base and (G) detail of two marginal teeth; H, *Eucithara stromboides* (Mangeliinae), a single hollow, harpoon-like marginal tooth; I, *Genota nicklesi* (Conorbinae), a single hollow, harpoon-like marginal tooth. nub, muscular bulb; rs, radular sac; sgl, salivary gland, vgl, venom gland. (A–C, after Taylor, J.D. *et al.* 1993; E, from Shimek & Kohn 1981)

[A–C, C. Eadie; D, F–I, courtesy of J.D. Taylor]

15. PROSOBRANCHS

All turrids are probably predatory, and polychaete annelids are the major prey of the 20 or so species for which diets are known. Less frequently, prey include sipunculans and nemerteans (Miller, B.A. 1990). As is probably typical of species-rich neogastropod families, where large numbers of species co-occur they tend to specialise on different prey species (Shimek 1983a, 1983b, 1983c). However, other turrid species, such as *Turricula nelli* which eats polychaetes of 17 different species, have more generalised diets (Taylor, J.D. 1985). Few direct observations of feeding behaviour are available, but prey capture in *Ophiidermella* (subfamily Borsoniinae according to traditional classification; Clathurellinae of family Conidae according to Taylor, J.D. *et al.* 1993) is essentially identical to that in *Conus* (Shimek & Kohn 1981; Shimek 1983b). *Turricula nelli* (subfamily Turriculinae according to traditional classification, Clavatulinae according to Taylor, J.D. *et al.* 1993), has a non-toxoglossate radula with three teeth per row that remain attached to the strong radular membrane. Nevertheless, it envenomates polychaetes externally and swallows them whole (Miller, B.A. 1990).

Information on the zoogeography of the family in Australia is probably best summarised at genus level. At least 85 genera are reported, in 13 subfamilies: Turrinae, Turriculinae, Borsoniinae, Drilliinae, Crassispirinae, Mangeliinae, Daphnellinae, Strictispirinae, Mitrolumninae, Taraninae, Conorbinae, Zonulispirinae and Thatcheriinae. The following subfamilies are not known to occur in Australia: Pseudomelatominae, Clavatulinae, Clathurellinae and Oenopotinae. J.D. Taylor *et al.* (1993) and Wilson (1994) gave the characteristics of each subfamily, and the latter author illustrated representative Australian species in each. About two-thirds of the genera occur in the southern zoogeographic province of Wilson & Gillett (1971) and about one-third in the northern province, including the overlap zones. The numbers of genera currently recorded by state are: New South Wales, 50; Victoria, 35; South Australia, 34; Tasmania, 26; Western Australia, 21; Queensland, 12. In contrast to the pattern in the more tropical Terebridae and Conidae, diversity is clearly higher in the southern province. Although the northern faunas appear to be the least well known, this diversity pattern is probably reasonably correct. For example, nearly 60% of the 180 species known from Queensland belong to the single subfamily Mangeliinae (Kay 1990).

Distributions of taxa are as yet too poorly known for estimation of the degree of endemism in the zoogeographic regions, but some indication can be gained from analysis of taxa recently revised by Wells (1990, 1991a, 1991b). All 15 Australian species of *Splendrillia* (subfamily Drilliinae) recognised by Wells are endemic. Wells (1990) originally reported that 12 of these were known from only one state, but subsequent information reduced this to 10 (Wells 1991b). All six Australian species of *Austrodrillia* are endemic and three are known only from South Australia (Wells 1990). In contrast, nine of 16 species of *Clavus* (subfamily Drilliinae) occur in other parts of the Indo-Pacific tropics as well as northern Australia (Wells 1991a).

Australian fossil Turridae number about 185 named species in 60 genera (Powell 1944; Valentine 1965; Darragh 1970, 1985; Long 1981).

Family Terebridae

The Terebridae exhibit the most homogeneous shell form of all three Conoidean families. Geographically and ecologically it is the most restricted family, occurring primarily on sand at shallow, subtidal depths circumtropically and in some subtropical regions. It is also the smallest family, with 265 extant species in four genera (*Terebra*, *Hastula*, *Duplicaria* and *Terenolla*) according to the recent systematic synthesis of Bratcher & Cernohorsky (1987). Although the results of more recent comparative anatomical study indicate incongruities in shell characters (Taylor, J.D. 1990), the current, less than satisfactory, diagnostic characters of the genera are as follows: *Hastula* – shell smooth and shiny, with axial sculpture of crenulations below the suture or slender ribs, without spiral sculpture except for a subsutural groove or punctations;

Duplicaria – shell with a subsutural groove cutting through the axial sculpture of ribs, without spiral sculpture or very weak spiral lines (Fig. 15.176A); *Terenolla* – shell small and straight-sided, with outer lip and columella rimmed with brown; placement in Terebridae is tentative; *Terebra* (Fig. 15.176B–E) – members of the family with features that are inconsistent with those of the other genera (Bratcher & Cernohorsky 1987).

The slender, elongate-conical terebrid shell is 10–270 mm in length, has a small last whorl, and consists mainly of the many-whorled spire (Fig. 15.176A–E). The aperture is small and has an anterior siphonal notch or very short canal (Fig. 15.176D). The posterior anal sinus (Fig. 15.176A, D) is shallow but usually distinct. The columella is thickened, twisted, and often bears folds or plaits (see Fig. 14.12). Shell material is added secondarily inside the early whorls. External sculpture commonly consists of narrow, closely spaced, collabral ridges. Spiral ridges or nodules may also occur. The shells of some species are smooth except for growth lines.

Terebrid morphology and physiology are discussed above under Conoidea. Members of the genus *Hastula* differ from other terebrids in having a large, flexible, fleshy foot with a broad propodium. They crawl rapidly on sand (20 to 30 steps/min) and use another locomotor method absent in other terebrids: the foot is extended broadly and functions as a sail that catches waves in the surf zone, carrying the animal rapidly up and down the beach (see Fig. 14.11; Miller, B.A. 1979).

Most terebrids are infaunal, burrowing to depths usually not exceeding the shell length in clean, fine to coarse sand in shallow subtidal habitats. Species of *Terebra* and *Duplicaria* usually occupy extensive sand bottoms, lagoons, or large sand patches on reef platforms. *Hastula* species often occur in or just below the surf zone on sloping sand beaches.

Reproduction has been studied only in one Hawaiian species each of *Terebra* and *Hastula*. In *T. gouldi*, males follow the mucous trails of females; the pair copulates while buried under the sand. The female attaches many stalked capsules containing six to eight eggs each to stones. Development is direct; benthic juveniles hatch 33 to 40 days after oviposition and burrow immediately (Miller, B.A. 1975). In *H. inconstans*, mating occurs on the sand surface while the pair rolls back and forth with the surge. Females attach egg capsules, about 1 mm across, to coarse sand grains of about the same size, just seaward of the surf zone. Each capsule contains about 40 eggs, and development is probably direct (Miller, B.A. 1979).

Foregut and radular morphology (Fig. 15.176F–H), and thus feeding mechanisms, vary widely in the family, but there are three main groups (Taylor, J.D. 1990). The first group has a short buccal tube and no venom apparatus, but has a well-developed radular ribbon bearing solid radular teeth (Fig. 15.176F – *Duplicaria* and *Pervicacia*; Rudman 1969). The second group has a long buccal tube forming a proboscis, venom apparatus, and hypodermic radular teeth (Fig. 15.176G – *Hastula* and some *Terebra* species, including *T. babylonia*, *T. guttata*, *T. subulata*; Taylor, J.D. 1990; Taylor, J.D. *et al.* 1993). The third group has a short buccal tube, no venom apparatus and no radula (Fig. 15.176H – some *Terebra* species, for example *T. gouldi*, *T. dimidiata*, *T. areolata*, *T. crenulata*, *T. maculata*). In *Hastula* (Miller, B.A. 1979), the proboscis is the extensile buccal tube, as in the Conidae. It carries a detachable, typically toxoglossate radular tooth at its distal end. This is injected into the prey, and venom from the tubular venom gland is pumped into the wound, the buccal tube contracts, and the prey is engulfed by the labial tube. Polychaete annelids, especially spionids, are the major prey items. In species of *Terebra* that completely lack radular and venom apparatus, the major prey items are the slow-moving enteropneust, *Ptychodera flava*, or polychaetes of the family Capitellidae. When the propodium contacts the prey, the labial tube everts and engulfs the worm, passing it to the buccal tube within. Swallowing is accomplished by alternate contractions and inversions of the buccal and labial tubes (Miller, B.A. 1975). Diets of species in the first group are the least well known, but include capitellid polychaetes (Taylor, J.D. 1990).

The thick shell of terebrids provides effective defence against predation, despite efforts by crabs especially of the family Calappidae. Even if the crab breaks the thin shell at the outer lip, *Terebra* can often withdraw into a portion of the whorl that is too thick for the crab to break. The shell is later repaired, but a jagged scar marks the site of the attack. In a sample of 133 individuals of five species of Australian *Terebra*, repairs following unsuccessful crab attacks averaged 0.9/shell (Vermeij, Zipser & Dudley 1980). In an experimental study, about half the attacks by *Calappa* on terebrid species with robust shells were successful, whereas most attacks on those with very slender shells were unsuccessful (Vermeij *et al.* 1980).

The Australian terebrid fauna includes at least 94 species, 71 in *Terebra*, 12 in *Duplicaria*, and 11 in *Hastula*, according to the generic classification of Bratcher & Cernohorsky (1987) and Wilson (1994). Three-quarters of Australian terebrid species occur

in the northern zoogeographic province of Wilson & Gillett (1971); 12% occur in the southern province, and the rest are in the eastern overlap zone. By states, the approximate numbers of known species are: Queensland, 56; Western Australia, 45; New South Wales, 19; South Australia, 10; Tasmania, 10; Victoria, seven (May 1921; Cotton 1952; Wells 1980b; Bratcher & Cernohorsky 1987; Wilson 1994). Of the northern group, 43 are Indo-Pacific and five (*H. rufomaculata*, *T. addita*, *T. crakei*, *T. marrowae* and *T. walkeri*) are endemic to Australia; the endemics all occur in Western Australia. All 11 southern province species (*D. fictilis*, *T. albida*, *T. assecla*, *T. bratcheriae*, *T. brazieri*, *T. flindersi*, *T. inconspicuus*, *T. kieneri*, *T. scalariformis*, *T. trilineata*, and *T. ustulata*) are endemic to Australia, as are seven of the 12 eastern overlap zone species (*T. bicolor*, *T. jacksoniana*, *T. praelongus*, *T. russetae*, *T. tristis*, *T. vallesia*, and *T. venilla*). Darragh (1970) lists 15 Australian Tertiary fossil species in seven terebrid genera.

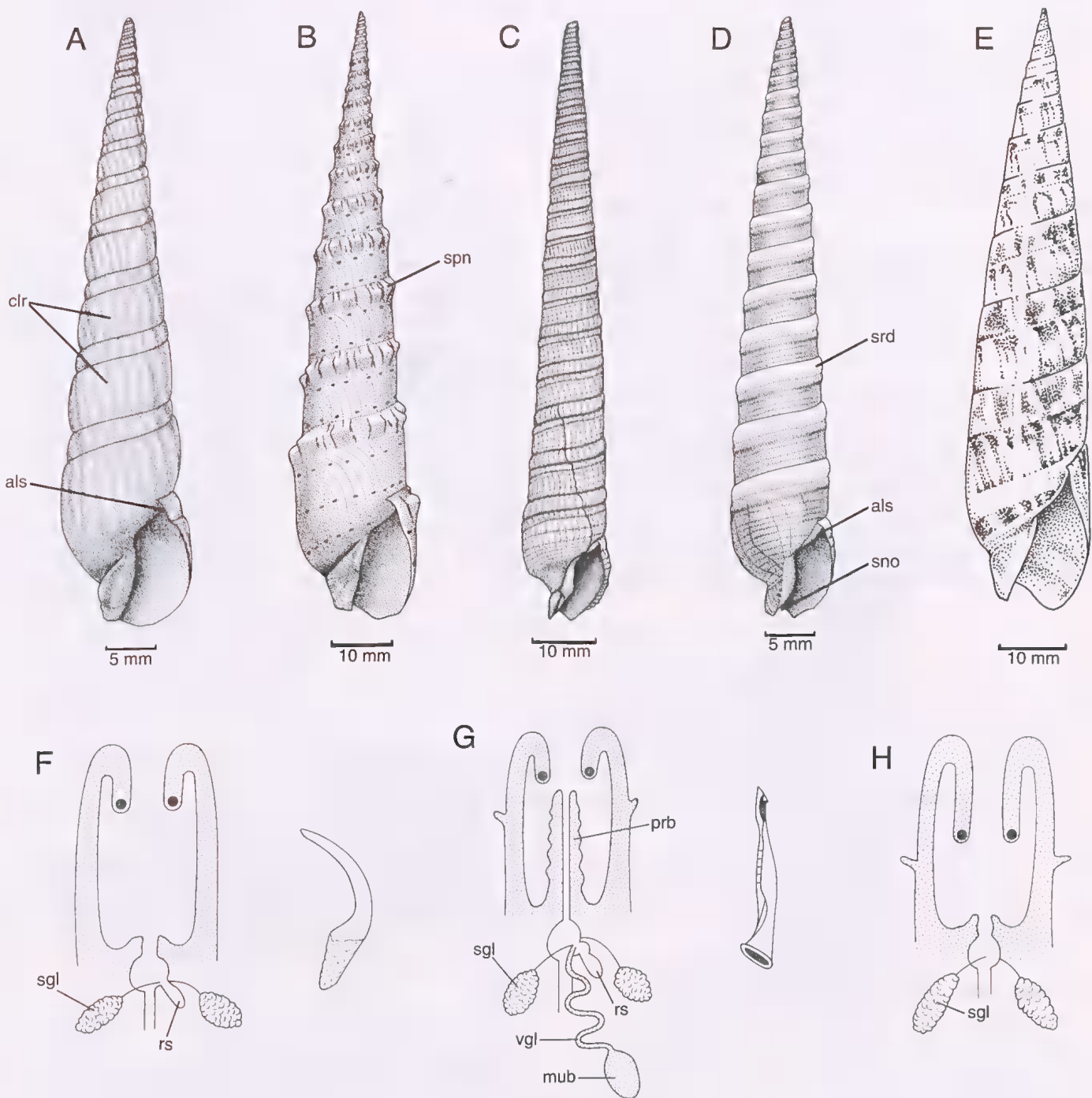


Figure 15.176 Family Terebridae. A-E, shells, apertural view: A, *Duplicaria evoluta*; B, *Terebra crenulata*; C, *Terebra lima*; D, *Terebra amanda*; E, *Terebra chlorata*. F-H, types of foregut morphology (in diagrammatic frontal section) and the type of radula associated with each: F, Type 1, *Duplicaria duplicaria*; G, Type 2, *Hastula cinerea*; H, Type 3, *Terebra dimidiata*. als, anal sinus; clr, collabral ridges; mub, muscular bulb; prb, proboscis; rs, radular sac; sgl, salivary gland; sno, siphonal notch; spn, spiral nodules; srd, spiral ridge; vgl, venom gland. (F-H, after Taylor, J.D. 1990) [A-D, F-H, C. Eadie; E, R. Plant]

Family Conidae

The family Conidae is primarily tropical, but a few species extend to latitudes beyond 40° in North America, Europe and Tasmania. The northern, warm-water Australian fauna includes primarily species typical of the Indo-West Pacific such as *Conus achatinus* (Fig. 15.177A) and *C. imperialis* (Fig. 15.177B). The southern Australian fauna by contrast includes primarily species that are endemic to this region such as *C. anemone* (Fig. 15.177C, E). A few species occur in both temperate and tropical regions of Western Australia but are endemic to the state, such as *C. dorreensis* (Fig. 15.177D). Conids occur from the intertidal zone to depths of several hundred metres. The family is generally considered to include the single genus *Conus* although some workers (for example Iredale & McMichael 1962) divide it into a number of genera. Wilson (1994) illustrated the 133 species known from Australia, and Röckel, Korn & Kohn (1995) provided a general account of Indo-Pacific *Conus*.

The shell is large (usually 20–200 mm long) and obconical or biconical (Fig. 15.177A–E). The last whorl is large, usually smooth or with low spiral lirae or striae anteriorly, and the aperture is long and narrow with the sides parallel or nearly so. The columella lacks folds or plaits except at the anterior extremity. The spire is smooth or bears fine spiral or axial sculpture; some species have a row of tubercles at the shoulder (Fig. 15.177B, D). Kohn & Riggs (1975) described shell morphometry and sculpture. An important internal characteristic of the *Conus* shell, differentiating it from shells of the closely related Turridae, is the nearly complete resorption of inner shell walls (Kohn, Myers & Meenakshi 1979). Shell colour patterns are often bright and complex (Pl. 29.4), but in life they are typically concealed (Pl. 29.5), either by an opaque periostracum or, in species with a thin, translucent periostracum, because the animal is inactive within sediment or under rocks during the day.

The most thorough anatomical studies of *Conus* are those of Bergh (1895) and Shaw (1914). Figure 15.177E illustrates the external features of an actively crawling individual. The large, muscular siphon extends forward from the anterior margin of the shell. The rhynchodeum also has thick, muscular walls. The paired tentacles arise from its sides, and each bears a small subterminal eye. The foot is elongate and the sole is rather quadrangular; the postero-dorsal surface bears a small, oblong operculum. Within the mantle cavity are the large ctenidium and large, complex osphradium (Spengler & Kohn 1995).

The major organs associated with feeding are shown in Figure 15.178A, and Figure 15.178B illustrates diagrammatically the foregut morphology. Within the rhynchodeum is the proboscis (Greene & Kohn 1989); the length of the proboscis when extended may exceed that of the shell. The elongate, tubular venom gland originates from one end of a large and very muscular bulb (Fig. 15.178A, B), and enters the anterior extremity of the oesophagus, just behind the entrance of the large, usually L- or V-shaped radular sac. The radular teeth are formed in the long right arm and stored in the compact left arm of the radular sac until each tooth enters the buccal cavity and proboscis prior to use (Fig. 15.178A). The oesophagus, stomach and intestine are as described for Conoidea. A representative radular tooth is illustrated in Figure 15.178C.

The earliest Australian specimens known were collected during Kerguelen's and Cook's voyages in 1773. The earliest *Conus* species based on an Australian specimen appears to be *C. puncturatus* Hwass, in Bruguière, 1792. Reportedly from Botany Bay, the described specimen has been lost, the description is inadequate, and the name is now considered a synonym of *C. sponsalis* (Kohn 1992). Other early species described from Australia include the endemic Western Australian *C. dorreensis* (Fig. 15.177D), collected at Shark Bay by Péron during the French expedition of 1800–1804, and *C. anemone*, described by Lamarck in 1810.

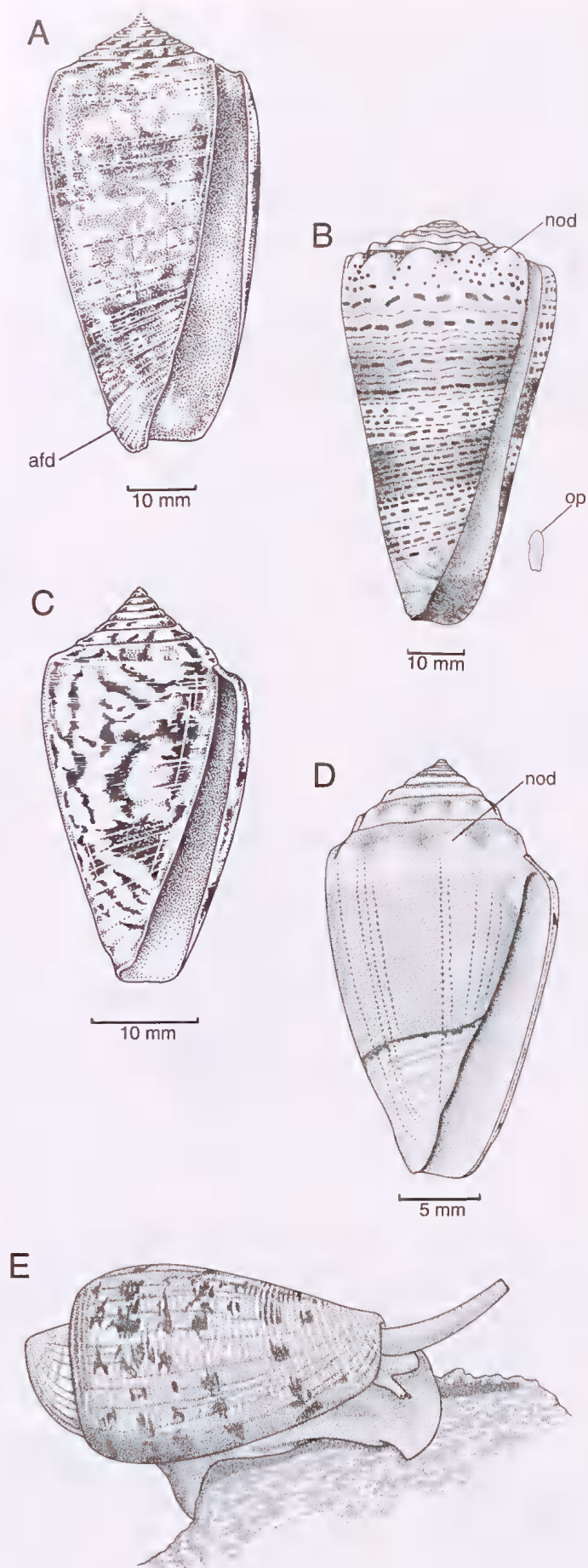


Figure 15.177 Family Conidae. Shells, apertural view: A, *Conus achatinus*; B, *Conus imperialis* with the small operculum at the same scale as the shell; C, *Conus anemone*; D, *Conus dorreensis*. E, *Conus anemone*, crawling animal, showing extended siphon, head (proboscis sheath, or rhynchodeum) with tentacles, and foot; the spire bears a commensal *Sabia australis* (Hipponicidae). afd, anterior folds at end of columella; nod, nodules on shoulder of shell; op, operculum. (E, after Wilson & Gillett 1971)

[A, C, R. Plant; B, D, E, C. Eadie]

Reproductive females deposit clusters of up to about 80 large, flask-shaped egg capsules (Kohn & Perron 1994; illustrations in Wilson & Gillett 1971), usually on the underside of a rock, or in sand-dwelling species, anchored within the substratum (Pl. 29.4). Each capsule contains from 30 to more than 20 000 eggs, depending on the species. Egg diameter ranges from 125–850 μm , and the total number of eggs in an egg mass ranges from a few thousand to 1.5 million (Kohn & Perron 1994). Oviposition has been observed in a few species on the reef at Heron Island, Queensland, in February and March (Frank 1969). Development to hatching usually takes 11 to 17 days. In most species, free-swimming, obligately planktotrophic veliger larvae hatch from the egg capsules. Benthic veliconchas or pediveligers hatch, usually after 18 to 26 days, in the few species with eggs more than 470 μm in diameter. Veligers that hatch from eggs slightly smaller than this are competent to settle and metamorphose after about a week in the plankton. Those developing from the smallest eggs must spend the longest time in the plankton, a minimum of about a month. All species that have been studied have shells about 1–2 mm long at metamorphosis (Kohn & Perron 1994).

In a study of growth and longevity of *Conus miliaris* at Heron Island, one year old individuals were estimated to have a shell length of 12 mm and to nearly double this during the next year. The modal age of the population was estimated at about three years; shell length at this age is about 30 mm (Frank 1969).

Most of the Australian species of *Conus* occur in coral reef habitats, but numerous species also occupy other marine environments such as intertidal and shallow subtidal coastal shorelines, deeper bays and lagoons, and offshore soft bottoms.

Ecological and behavioural information is available only for reef and shallow-water species (for example, Kohn 1959, 1968; Kohn & Nybakken 1975). Active nocturnally, most *Conus* are quiescent during the day, often sheltered under rocks or algae or buried in sediment. For example, *C. ebraeus* at One Tree Island, Queensland, moved about actively at night but remained inactive in protected sites during daylight hours (Leviten & Kohn 1980). The availability of refuges is an important determinant of *Conus* species diversity and population density in topographically smooth, intertidal habitats; Kohn & Leviten (1976) gave data for One Tree Island.

On coral reef platforms, diversity and density of *Conus* species are directly correlated with the presence of appropriate substratum type, such as patches of sand bound by algal filaments, and are inversely correlated with living coral cover (Kohn 1983). As many as 25 to 30 species co-occur on Great Barrier Reef platforms. Where gradients of substratum types occur on these platforms, the *Conus* species show a characteristic pattern of zonation (Reichelt & Kohn 1985).

Feeding in *Conus* species usually occurs during the nocturnal active period. Prey organisms are swallowed whole after being stung and paralysed by venom injected by a hollow, harpoon-like radular tooth (Figs 1.14E, 15.178B, C). Prior to feeding, one tooth is moved to the distal end of the proboscis. When the tip of the proboscis contacts a suitable food organism, its musculature injects the tooth into the prey, while the proboscis lip grasps the posterior end of the tooth. The paralysed prey is then engulfed, as described for the superfamily Conoidea. Reichelt & Kohn (1985) and Kohn & Almasi (1993) summarised data on the diets of 28 Australian species. Twenty-four of these, among them *C. imperialis* (Fig. 15.177B), *C. anemone* (Fig. 15.177C, E), *C. dorreensis* (Fig. 15.177D), and *C. lividus* prey on polychaete worms of 13 families. *Conus marmoreus*, *C. textile* and related species prey exclusively on other gastropods, and *C. achatinus* (Fig. 15.177A), *C. geographus*, *C. tulipa*, *C. striatus*, and *C. catus* prey only on fishes (see illustration in Wilson & Gillett 1971). Species in the last group are particularly dangerous to humans (see Sutherland 1983). At least four human injuries from *Conus* stings have occurred in Australia, one of which, by *C. geographus*, was fatal (Flecker 1936). More than 100 human injuries, of which more than 30 were

fatal, have occurred throughout the world. Lewis, Alewood, Dooley, Martin, Drinkwater *et al.* (1996) are researching cone shell venom for new bioactive peptides; these peptides will form the basis for developing drugs to treat stroke and pain.

If the broad marine zoogeographic classification of Australia adopted by Wilson & Gillett (1971) is applied, 76% of the 126 known Australian *Conus* species occur in the northern province (= NE + NW oceanic zones, see Smith, B.J. 1992), 14% in the eastern overlap zone (= Central and Lower east coast zones), 8% in the western overlap zone (= W oceanic zone) and 2% in the southern province (= S + SE oceanic zones; two extend to the W oceanic

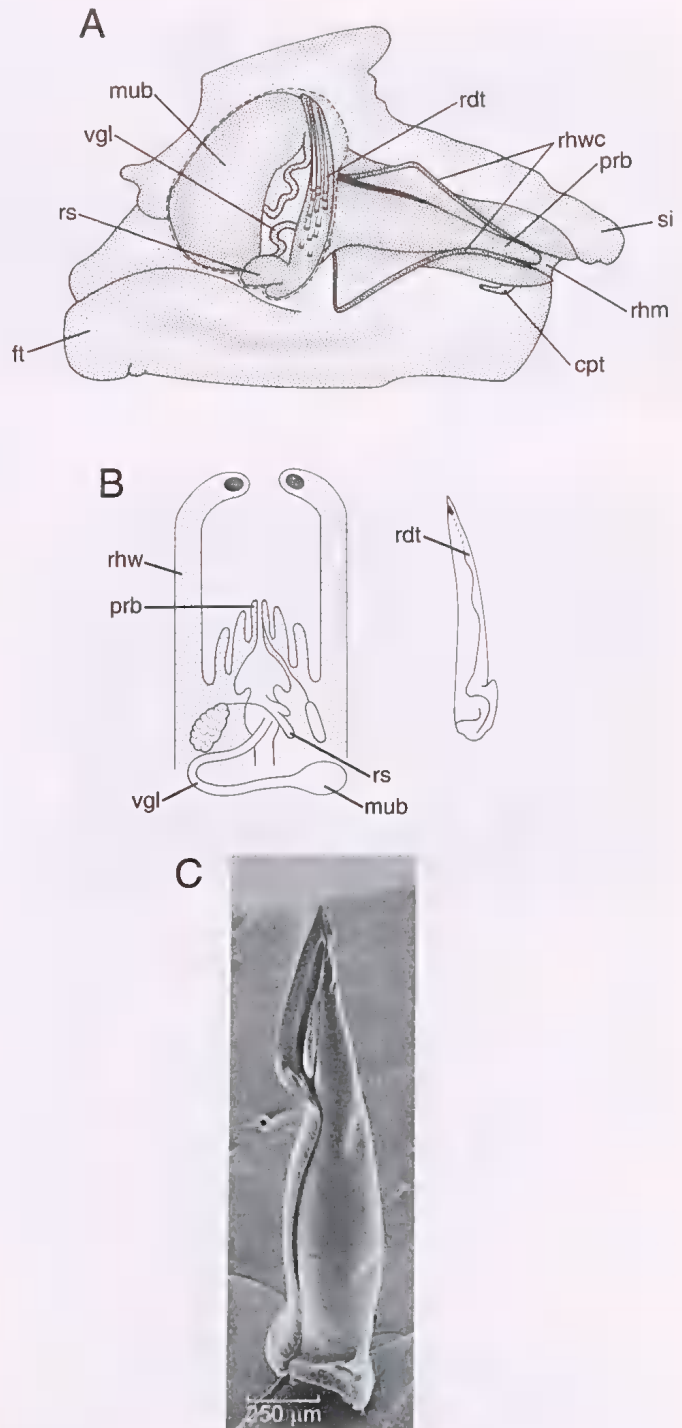


Figure 15.178 Family Conidae. A, *Conus striatus*, dissected from the dorsal side of the rhynchodeum and the anterior part of the body cavity (dotted line). B, foregut morphology in *Conus* (diagrammatic frontal section) and associated type of radular tooth. C, radular tooth of *Conus imperialis*. cpt, cephalic tentacle; ft, foot; mub, muscular bulb of venom apparatus; prb, proboscis; rdt, radular teeth forming in right arm of radular sac; rhm, rhynchostome; rhw, rhynchodeal wall; rhwc, rhynchodeal wall cut and folded back; rs, radular sac; si, siphon; vgl, venom gland. (A, Kohn unpublished; B, after Taylor, J.D. *et al.* 1993; C, from Kohn, Nybakken & Van Mol 1972)

[A, B, C. Eadie]

15. PROSOBRANCHS

zone). By states, the approximate numbers of known species are: Queensland, 94; Western Australia, 69; New South Wales, 16; South Australia, 3; Victoria, 3; Tasmania, 2. All 17 species of the eastern overlap zone are endemic (for example, *C. advertex*, *C. howelli*, *C. minnamurra*), and numerically are more than half the known Australian endemic *Conus* species. Nine of the 13 southern and western zone species are endemic (*C. anemone*, *C. clarus*, *C. dampierensis*, *C. dorreensis*, *C. gabelishi*, *C. klemae*, *C. nodulosus*, *C. rutilus*, and *C. reductaspiralis*), but only three species (3%) of all the northern zone species are endemic (*C. austroviola*, *C. cyanostoma* and *C. trigonus*). The small number of northern endemics is to be expected, as most species in this region are widely ranging Indo-West Pacific species. One eastern Australian species, *C. howelli*, is also recorded from Lord Howe Island and northern New Zealand (Marshall 1981).

The genus *Conus* probably originated early in the Tertiary. The oldest Australian fossils are Oligocene; most of the 16 extinct species (Darragh 1970) occur in that epoch. The fossil record indicates that on a worldwide basis the genus experienced major radiations in the Eocene and Miocene (Kohn 1985). Three Australian Eocene species extend into the Miocene, but no species are known to have originated in the Miocene. One species is known only from the Pliocene, and one extant species, *C. anemone*, is also known as a Pliocene fossil (Dennant & Kitson 1903). The modern high diversity of coral reef-dwelling species may represent colonisation from the north as the Indo-Australian plate moved northward in the Neogene.

Superorder HETEROBRANCHIA

Heterobranchia is a group of equal rank to Caenogastropoda and encompasses the Opisthobranchia and Pulmonata as well as some taxa previously treated as prosobranchs. The concept of Heterobranchia as used here was introduced by Haszprunar (1985b, 1988a). It is a clade including Valvatoidea, Architectonicoidea and other groups, such as the Pyramidellidae, which were included in the paraphyletic 'Heterostropha' by Ponder & Warén (1988), as well as the large and diverse euthyneuran groups, Opisthobranchia and Pulmonata, treated in the next two chapters.

The combination of pulmonates and opisthobranchs into a single grouping Euthyneura was advocated by several workers (Spengel 1881; Boettger 1954; Zilch 1959–1960; Taylor, D.W. & Sohl 1962). Haszprunar's (1985b, 1988a) concept of Heterobranchia included the euthyneuran groups and 'prosobranch-like' taxa which he grouped as Triganglionata (Haszprunar 1985b) or Allogastropoda (Haszprunar 1985d). This same paraphyletic grouping was referred to as Heterostropha by Golikov & Starobogatov (1975, in part) and Ponder & Warén (1988), and the name was used, but differently, by Bandel (1990, 1991) as equivalent to the Heterobranchia. Bieler (1992a) reviewed the recent taxonomic changes in the Heterobranchia and discussed current ideas on relationships. The systematic position and complicated taxonomic history of architectonicids, omalogyrids, rissoellids and pyramidellids have been discussed in detail by Haszprunar (1985b, 1988a), Bieler (1992a) and Huber (1993).

The heterobranch clade is supported by many synapomorphies (Haszprunar 1985b, 1988a; Ponder & Lindberg 1997), including the sinistral larval shell produced by a planktotrophic veliger. Some synapomorphies of this clade, such as pigmented mantle organ, no ctenidium, simple oesophagus and lack of odontophoral cartilages, are probably due to secondary loss or simplification as result of paedomorphic processes (Ponder & Lindberg 1997). Other synapomorphies, at least of many primitive heterobranchs, include the medial position of the eyes relative to the tentacular bases and opposed ciliated ridges in the pallial cavity.

Heterobranchia is probably a monophyletic group consisting of several ancient evolutionary lines, many of which have only a few extant taxa. However, the monophyly of several currently recognised groupings within Heterobranchia is equivocal.

'Heterostropha' is clearly paraphyletic and Opisthobranchia, which has few if any obvious synapomorphies, may also be paraphyletic (Haszprunar 1985b). Most pulmonates, on the other hand, are distinguished by their pulmonary cavity and all supposedly have a procerebrum (Van Mol 1967; Haszprunar 1988a; Haszprunar & Huber 1990). These two characters have recently been shown to be homologous with the mantle cavity and the tentacular ganglion (Ruthensteiner personal communication), respectively, of other gastropods. Recent molecular studies (Tillier *et al.* 1994) have suggested that the Pulmonata may also be paraphyletic. Neither a pulmonary cavity nor procerebrum is present in the Glacidorbidae, a family included with pulmonates by Ponder (1986b), in the 'Allogastropoda' (*i.e.* Heterostropha) by Haszprunar (1988a) and in a separate 'order' (Glacidorbiformes) in the 'subclass Sinistrobranchia' by Starobogatov (1988). Unpublished sperm data (J.M. Healy personal communication) suggest relationships with basal pulmonates (where glacidorbids are included in this volume), and if this is valid, glacidorbids are presumably highly paedomorphic.

There is no general agreement on the sister group of heterobranchs. Several workers (for example, Boettger 1954; Fretter & Graham 1962; Brace 1977a, 1977b; Fretter 1980; Gosliner 1981; Schmekel 1985) suggested that the opisthobranch–pulmonate clade (Euthyneura) was derived from the lower 'mesogastropods' and J.E. Morton (1955b) suggested a monotocardian 'archaeogastropod' origin. The derivation of Heterobranchia from an 'archaeogastropod' grade was also suggested by Ponder (1991a) and is supported by the finding of rhipidoglossate-like radulae in some recently named valvatoidean groups (Warén *et al.* 1993). Derivation of Architectonicoidea from the 'archaeogastropod' euomphalids (for example, Knight *et al.* 1960b; Dzik 1982; Bandel 1988) on the basis of protoconch morphology has also been suggested, but support from the fossil record for the derivation of Heterobranchia is inconclusive. Indisputable heterobranchs first appear in the fossil record in the Lower Carboniferous (Kollmann & Yochelson 1976; Yoo 1994).

Analysis of sperm ultrastructure suggests that heterobranchs do not share a common ancestry with extant caenogastropods, vetigastropods or neritopsines (Healy 1993a). Heterobranchia appears to be a paedomorphic group that evolved in parallel with other gastropod lineages since its origin deep in the Palaeozoic and some synapomorphies (mostly sperm characters, Healy 1993a) suggest a common ancestry with caenogastropods.

In the treatment below, the plesiomorphic heterobranch taxa included in the 'Allogastropoda' (Haszprunar 1988a) or 'Heterostropha' (Ponder & Warén 1988) are dealt with at the superfamily level because this grouping is clearly paraphyletic. Their shared similarities are all plesiomorphies – coiled shell and operculum, streptoneury or partial streptoneury, well-developed pallial cavity with opposed ciliated ridges, cephalic tentacles, *etc.* Following these superfamilies, are major introductions, in separate chapters, to the Opisthobranchia and Pulmonata. These groups are not treated as subclasses here. For those who prefer taxa to be ranked, Heterobranchia can be treated as a superorder, although some recent reviews (for example, Haszprunar 1988a; Ponder & Warén 1988) have treated it as a subclass. The latter approach, to be consistent, would require the elevation of all the groups which we regard as superorders to subclass.

Superfamily VALVATOIDEA

The Valvatoidea is a small superfamily based on a Northern Hemisphere freshwater group which has only very recently been extended to include marine families (Ponder 1990b, 1990c, 1991a; Bandel 1991; Warén *et al.* 1993). The group is distinguished from other 'Heterostropha' in possessing a snout, a pallial tentacle, microphagous feeding, a style sac, an external penis, and a well-developed radula with at least five teeth in each row (rhipidoglossate-like in some taxa), and in the ultrastructure of the sperm (see Healy 1991 for details).

Valvatoid shells are trochiform to discoidal, variously sculptured, with a slightly heterostrophic protoconch (Bandel 1991; Warén *et al.* 1993), or if development is direct, the protoconch is non-heterostrophic.

The shell aperture is simple. The operculum is simple and circular with a central nucleus. The head bears a pair of long, slender tentacles with eyes in the middle of their bases. There is a single or double posterior pallial tentacle, often long. A well-developed anterior pedal gland opens at the anterior edge of the foot and a

posterior pedal gland maybe present or absent (present in orbitestellids). The foot is either simple or has the anterior edges and/or posterior parts produced into long extensions. There are no metapodial or epipodial tentacles.

The pallial cavity has an osphradium, sometimes well developed and a bipectinate, secondary (Rath 1988) gill may be present. The secondary gill, when present, often projects from the aperture. A pigmented mantle organ is present or absent (present in Orbitestellidae and possibly Cornirostridae).

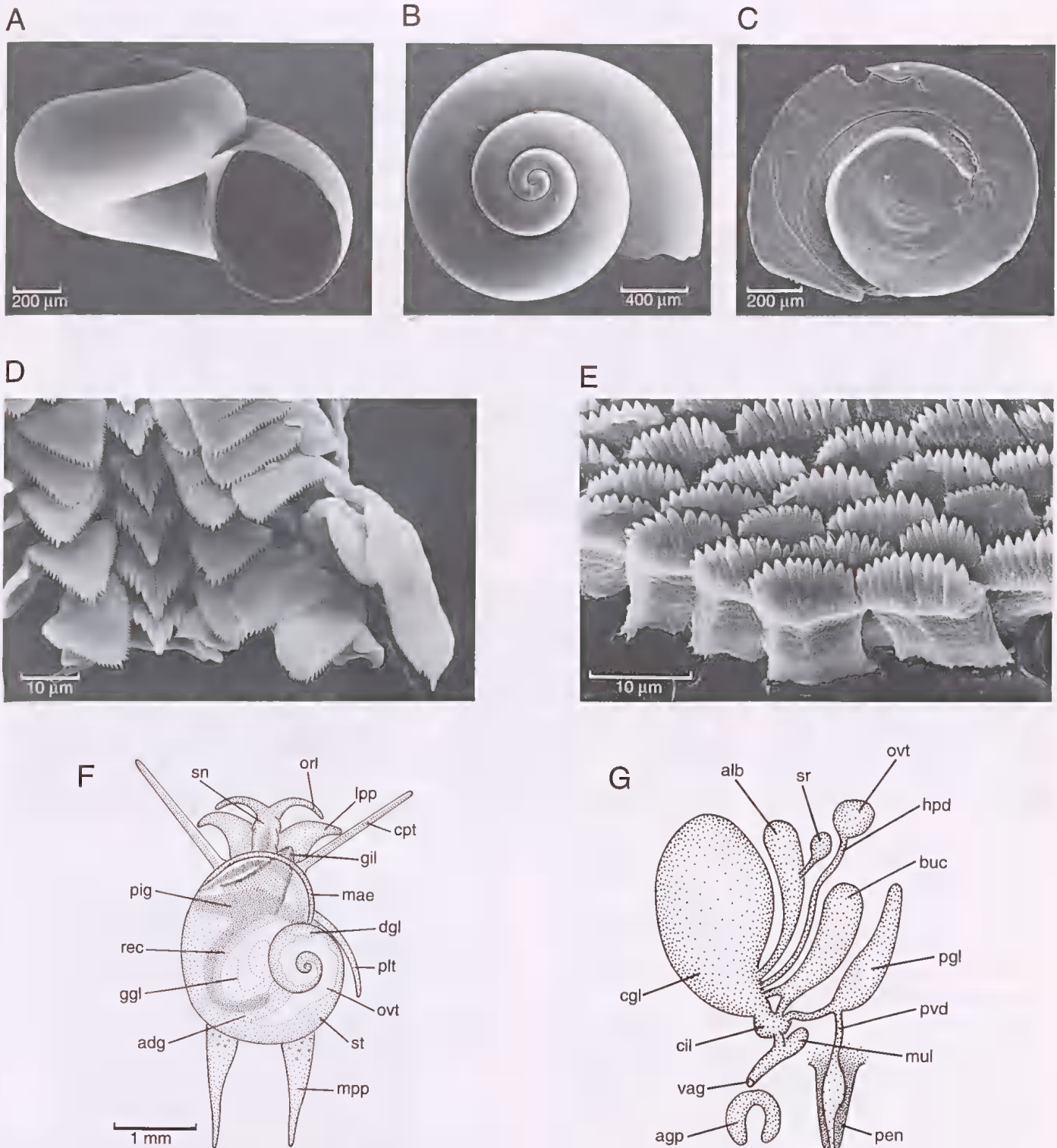


Figure 15.179 Family Cornirostridae. *Cornirostra pellucida*: A, shell, apertural view; B, shell, dorsal view; C, operculum, outer surface; D, portion of radula, showing central teeth and lateral teeth on left, and lateral and marginal teeth on right; E, serrated jaw elements; F, living animal, dorsal view; G, diagram of reproductive system. *adg*, anterior digestive gland; *agp*, anterior glandular pocket; *alb*, albumen gland; *buc*, bursa copulatrix; *cgl*, capsule gland; *cil*, ciliated sac; *cpt*, cephalic tentacle; *dgl*, posterior digestive gland; *ggl*, pallial genital gland; *gil*, gill; *hpd*, hermaphroditic duct; *lpp*, lateral extension of propodium; *mae*, reflected mantle edge; *mpp*, metapodial process; *mul*, muscular pocket; *orl*, lateral extension of snout (oral lobe); *ovt*, ovotestis; *pen*, penis; *pgl*, prostate gland; *pig*, pigment on the pallial roof; *plt*, pallial tentacle; *pvd*, pallial vas deferens; *rec*, rectum; *sn*, snout; *sr*, seminal receptacle; *st*, stomach; *vag*, vagina. (F, G, after Ponder 1990b)

[A–E, W.F. Ponder; F, G, C. Eadie]

15. PROSOBRANCHS

A pair of lateral jaws is present, each composed of few to many discrete plates. The radula either superficially resembles a taenioglossan type (with seven tooth rows), or is reduced to five tooth rows, with eight teeth in each row (in Orbitestellidae), or is rhipidoglossate-like (Warén *et al.* 1993) with numerous marginal teeth. The oesophagus is simple, except for low dorsal folds in the anterior part in *Cornirostra*. A style sac (which in orbitestellids contains a crystalline style) is present and the anus lies anteriorly in the pallial cavity in valvatids and cornirostrids, but is placed posteriorly in orbitestellids as in other Heterostropha. The kidney is situated largely in the pallial roof. The nervous system is epiathroid and exhibits streptoneury. Valvatoideans are hermaphrodites, and the accessory structures of the female part of the reproductive system, including the large capsule gland and the anteriorly situated vagina, are mostly pallial. The male system includes a pallial prostate gland and an external penis which lies behind the right eye. Healy (1990e) has described the sperm of members of the superfamily and has shown that they differ from those of other heterobranchs, possessing some synapomorphies, that support the cohesion of this group.

Larval development is apparently direct in most taxa but a few have planktonic larvae (Warén *et al.* 1993, personal observation). Egg capsules are known in only two groups. *Valavata* species have rounded capsules containing a few eggs connected by chalazae (Clealand 1954) and species of *Cornirostra* have spiral egg masses composed of firm, transparent material with 200+ eggs (Ponder 1990c).

Little is known about the biology of marine valvatoideans, although stomach contents suggest that they feed microphagously (Ponder 1990b, 1990c), as do the freshwater Valvatidae.

The composition of the Valvatoidea is still under review because all the families (other than Valvatidae) have been added subsequent to Ponder's review in 1990c. It consists of at least four families, three of which are found in Australia (Orbitestellidae, Cornirostridae and Xylodisculidae). The taxonomic position of the Valvatidae has been in dispute. Valvatids were usually regarded as primitive 'mesogastropods', but were recently shown to be basal heterobranchs (Salvini-Plawen & Haszprunar 1987; Haszprunar 1988a; Rath 1988).

Little is known of the fossil history of valvatoideans, but Ponder (1990b) reports a Jurassic orbitestellid from New Zealand and Bandel (1988) has discussed the similarities of orbitestellids to some Mesozoic taxa previously grouped in the Euomphaloidea.

This group is of special phylogenetic interest because of its basal position in the Heterobranchia (see Ponder 1991a for discussion).

Family Cornirostridae

Cornirostrids have small, depressed-trochiform, smooth, usually umbilicate shells with a wide umbilicus and a flat to slightly raised spire (Fig. 15.179A, B). The radula has nine teeth in each row (Fig. 15.179D) and the jaws are small and composed of many serrated elements (Fig. 15.179E). The large stomach has a style sac but there is no crystalline style. A long posterior pallial tentacle is present. The head bears long cephalic tentacles and an external penis on the right side.

The family Cornirostridae was described by Ponder (1990c) and the information that follows is mainly obtained from that paper. The shells of cornirostrids are tiny (less than 3 mm in diameter) and depressed trochiform, closely resembling those of some vitrinellids. The aperture is simple, with a thin, evenly-curved peristome. The protoconch is paucispiral (about one and a quarter whorls). The operculum is circular and multispiral with a central nucleus (Fig. 15.179C).

The head bears a bilobed snout (Fig. 15.179F), the lobes produced into tentacle-like lateral extensions, and a pair of long cephalic tentacles with eyes in the middle of their bases. An external penis lies below the base of the right tentacle. A long pallial tentacle arises from the mantle in the posterior (dorsal)

corner of the aperture. The foot is long, the anterior end having the lateral corners extended into narrow processes and the posterior end produced into a pair of long 'tails' (Fig. 15.179F). Movement is by ciliary gliding.

The pallial cavity contains a large bipectinate gill which is attached anteriorly and projects forwards. There is an anterior pigmented area in *Cornirostra* which may be, at least in part, a pigmented mantle organ but there is no trace of this in the American genus *Tomura*.

A pair of jaws are made up of numerous small, serrated elements (Fig. 15.179E). The radula has nine teeth in each row, the central teeth having long lateral projections and sharp denticles on the triangular cutting edge (Fig. 15.179D). The lateral and marginal teeth have numerous very small denticles. There are two pairs of lateral and two pairs of marginal teeth – the two lateral teeth were interpreted as being a single unit by Ponder (1990c), but were shown to be two separate teeth by Warén *et al.* (1993). The oesophagus is simple and the large stomach has a short style sac. The stomach contents have been reported to include unicellular plants and detritus (Ponder 1990c).

The heart lies at the base of the pallial cavity behind the kidney. The nervous system is rather concentrated, with the cerebral and pleural ganglia abutting, and with short cerebral and pedal commissures. The supra-oesophageal ganglion has a short connective to the right pleural ganglion and the suboesophageal ganglion abuts the left pleural ganglion. The hermaphrodite reproductive system is rather complex (Fig. 15.179G). It is generally similar to that of Valvatidae, with large, mainly pallial oviduct glands and prostate, and an anterior glandular pocket which is possibly utilised in spawn formation. There is an external penis on the right side of the head.

Cornirostrids live in the intertidal zone in sheltered, fully marine water, sometimes in estuaries or sheltered bays or pools, often beneath stones or other objects but sometimes on seagrasses.

Cornirostra is the only known genus in this family in the Australasian region and another genus, *Tomura*, is known from Florida, United States of America. Nothing is known of cornirostrid fossil history, but Bandel (1991) has suggested that his Provalvatidae (Upper Jurassic to Lower Cretaceous), which may be ancestral to the Valvatidae, might be descended from the Cornirostridae.

A related group, placed in a separate family, Hyalogryinidae, has a rhipidoglossate radula and includes three genera, *Hyalogryrina* and *Hyalogyra*, species of which live on sunken wood in the deep sea or in hydrothermal vents (Marshall 1988b; Warén & Bouchet 1993), and *Xenoskenea* (Warén *et al.* 1993) based on a shallow-water Mediterranean species. Species of *Xenoskenea* are also known from New Caledonia (A. Warén personal communication) and Australia (New South Wales and southern Western Australia; W.F. Ponder personal observation), and produce egg masses identical to those of *Cornirostra*. One species of *Hyalogryrina* and one of *Hyalogyra* are known from deep water (800 m to greater than 1000 m) on sunken wood from New Zealand (Marshall 1988). Anatomical investigations currently under way by G. Haszprunar will assist in establishing the relationships of these taxa.

Family Orbitestellidae

Orbitestellids have minute, discoidal, smooth to elaborately sculptured shells with a wide umbilicus and a flat to slightly raised spire (Fig. 15.180A, B, D, E). The radula has five teeth in each row (Fig. 15.180F) and the jaws are very large and composed of long serrated elements (Fig. 15.180C). The large stomach contains a crystalline style. A double posterior pallial tentacle is present. The head bears long cephalic tentacles and an external penis on the right side.

Orbitestellids were not separated from other small, low-spired shells usually included in the Liotiidae, Skeneidae or Vitrinellidae until Iredale (1917b) named the family on the basis of shell characters. It was regarded as a member of the Trochoidea (for example, Thiele 1929–1935; Wenz 1938–1944; Knight *et al.* 1960c) until Ponder (1967) placed it in the Rissooidea on the basis of the radula and external features of the animal. He also included *Microdiscula* in the Orbitestellidae on the basis of the description of the radula and jaw published by Thiele (1912). Ponder & Warén (1988) included the family in the Valvatoidea on the basis of anatomical features (Ponder 1990b). Most of the information summarised below is from Ponder (1990b).

Orbitestellid shells are tiny (less than 3 mm in diameter) and have a flat to slightly raised spire. *Microdiscula* species are either smooth or very weakly sculptured with axial or spiral threads (Fig. 15.180D, E). *Orbitestella* species are sculptured with a few spiral ridges that are often rendered nodulose by axial riblets or threads crossing them (Fig. 15.180A, B). The aperture is sinuate,

with a distinct posterior (dorsal) notch, a weak (*Microdiscula*) to strong subperipheral notch and an anterior (ventral) notch. The protoconch is paucispiral, having 1.3–1.5 whorls. The operculum is circular, multispiral with a central nucleus.

The head bears a bilobed snout and a pair of long cephalic tentacles with large eyes in the middle of their bases (Fig. 15.180G). The hermaphrodite reproductive system is simple, and has a pallial oviduct gland and a prostate gland. An external penis lies below the base of the right tentacle. A rather short, double pallial tentacle arises from the mantle in the posterior (dorsal) corner of the aperture. The foot is short, with an anterior and posterior pedal gland, and movement is by ciliary gliding.

The pallial cavity lacks a gill, but a large osphradium lies obliquely across the left side of the pallial roof. There is a densely pigmented mantle gland in the anterior pallial roof, behind which lies the kidney. A ciliated tract runs from the posteriorly located anus along the right side of the pallial cavity.

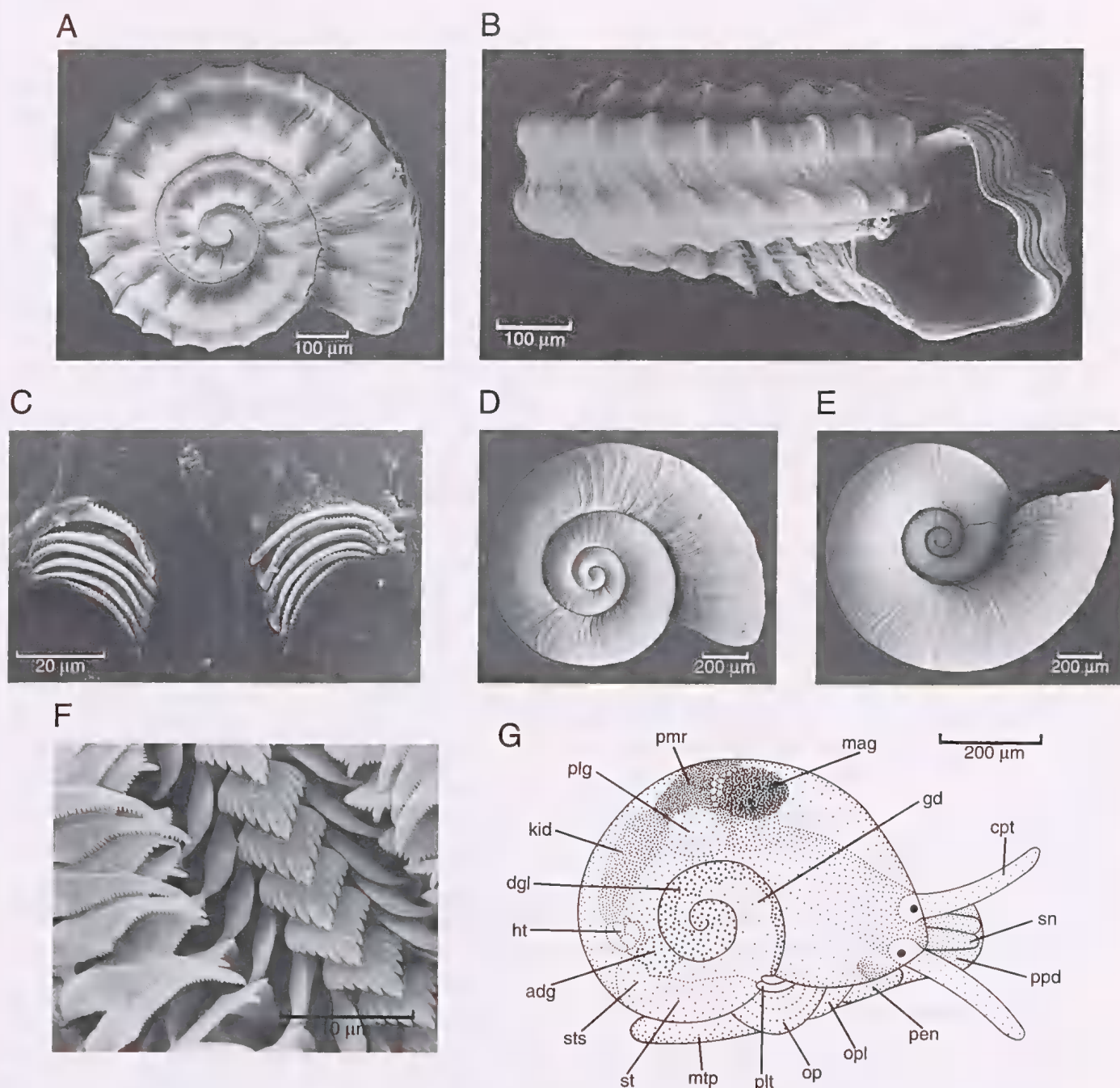


Figure 15.180 Family Orbitestellidae. A–C, *Orbitestella decorata*: A, shell, dorsal view; B, shell, apertural view showing sinuate outer lip; C, jaws. D–G, *Microdiscula charopa*: D, shell, dorsal view; E, shell, ventral view; F, portion of radula, showing central teeth and portions of the lateral and marginal teeth on left and right; G, animal, dorsal view of exterior. adg, anterior digestive gland; cpt, cephalic tentacle; dgl, posterior digestive gland; gd, gonad; ht, heart; kid, kidney; mag, mantle gland; mtp, metapodium; op, operculum; opl, opercular lobe; pen, penis; plg, pallial genital gland; plt, pallial tentacle; pmr, pigment on pallial roof; ppd, propodium; sn, snout; st, stomach; sts, style sac. (G, after Ponder 1990b)

[A–F, W.F. Ponder; G, C. Eadie]

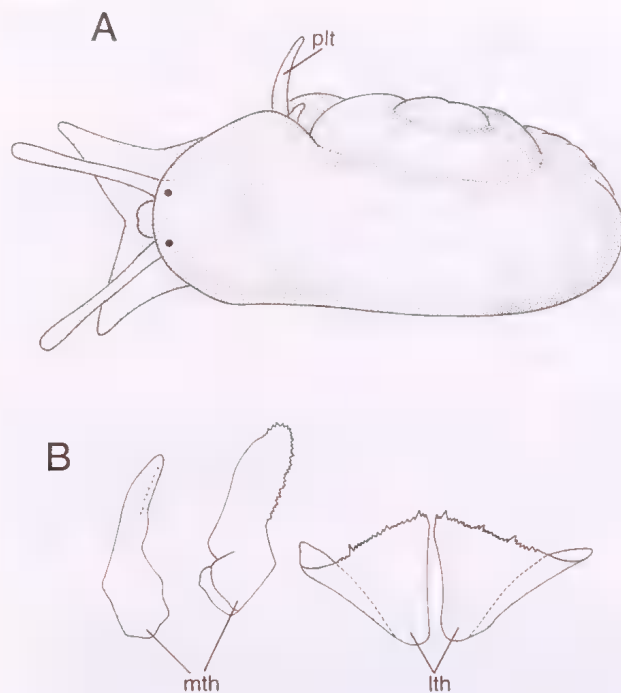


Figure 15.181 Family Xylodisculidae. *Xylodiscula boucheti*: A, external appearance; B, portion of radular tooth row, showing the fan-shaped lateral teeth and two marginal teeth (the central tooth is absent). lth, lateral teeth; mth, marginal teeth; plt, pallial tentacle. (A, B, after Warén 1992)

[A, B, C. Eadie]

The large jaws are diagnostic for the family (Fig. 15.180C). They lie on each side of the oral tube and are composed of several vertical rows of paired long, serrated elements; in *Microdiscula* there are three additional smaller elements in each row. The radula is small relative to the jaws and contains five teeth in each row; the central teeth have long lateral projections and sharp denticles on the triangular cutting edge. The lateral and marginal teeth have numerous, very small denticles (Fig. 15.180F). The oesophagus is simple and the large stomach contains a short crystalline style, this being unique among Heterobranchia. The stomach contents include unicellular plants and detritus.

The heart lies at the base of the pallial cavity behind the kidney. The nervous system is concentrated, with the cerebral and pleural ganglia fused and the cerebral and pedal commissures virtually absent. The supra-oesophageal ganglion abuts the right pleural ganglion and the suboesophageal ganglion is separated by a short connective from the left pleural ganglion.

Orbitestellids live in the lower littoral and sublittoral zones; species of *Orbitestella* usually live amongst rubble and beneath stones whereas species of *Microdiscula* are usually associated with algae.

Orbitestellids are known virtually worldwide. Few species are named, however, and many remain undescribed. At present it appears that the greatest diversity occurs in Australasia. They are known from as early as the Jurassic in New Zealand (Maxwell in Ponder 1990a) and the Eocene of Europe and Australia. Bandel (1988) has discussed similarities of orbitestellids to some Mesozoic taxa previously grouped in the Euomphaloidea.

Family Xylodisculidae

Xylodisculids are small gastropods with smooth, simple planorboid shells, sometimes with a weak peripheral angulation (Fig 15.181A). A hyperstrophic protoconch is present in those assumed to have planktotrophic development. The animal has an anteriorly bifid foot, long cephalic tentacles with eyes in the middle of the bases, a short snout and a pair of posterior pallial tentacles, one of the pair long.

The radula (Fig. 15.181B) has the formula 2-1-0-1-2, the lateral teeth being fan-shaped, with a wide, multicuspidate cutting edge. The two marginal teeth are narrow and weakly denticulate. Jaws are apparently lacking, in contrast with the Orbitestellidae. Further details of anatomy are unknown.

This small family was recently established (Warén 1991b) for a species described from off New South Wales by Marshall (1988b). Only a few species are known, three from deep water (440 m to over 1000 m) off New South Wales and New Zealand where they live on sunken wood (Marshall 1988b), and two from the Mediterranean Sea in 90–120 m associated with dead seagrass (Warén 1991b). The operculum is described as 'absent' in one species, and not mentioned in descriptions of the other taxa.

Superfamily ARCHITECTONICOIDEA

Architectonicoideans are marine, operculate heterobranchs with discoidal to turreted adult shells, heterostrophic or anastrophic protoconchs, and various buccal specialisations for feeding on colonial cnidarians (including corals). The superfamily comprises the Architectonicidae (sundial shells) and Mathildidae.

Study of Australian Architectonicoidea has centred chiefly on comparative shell morphology, although the anatomy of some species known to occur in Australian waters has been examined (see Climo 1975; Bieler 1993). Architectonicoideans from the east coast have been described, from shells, by Tate (1893b), Hedley (1903, 1907), Iredale (1929b, 1931, 1936a, 1957) and Garrard (1961, 1977). Allan (1959) indicated shell features and distributions of the more commonly encountered architectonicids from Australia, but provided little information on living animals. Garrard (1977) reviewed the extant and fossil Architectonicidae of Australia, incorporating data on opercula and depth ranges. Most recently, the Australian Architectonicidae have again been reviewed, this time as part of a detailed monograph by Bieler (1993) on the family in the Indo-Pacific. Laserson (1951b) gave a comparative account (shells only) of mathildids from New South Wales, but a subsequent study (Bieler 1995) has shown that several of these species are in fact referable to various caenogastropod families. Bieler (1995) suggested the use of *Mathilda sensu lato* in preference to the current use of numerous nominal genera (for example *Eucharilda*, *Opimilda*).

The shells of architectonicoideans are sculptured and variable in form, ranging from discoidal or trochoidal (Architectonicidae, Fig. 15.183A) to high spired (most Mathildidae, Fig. 15.182A, B). The umbilicus is wide (Architectonicidae), or is narrow or absent (Mathildidae). The protoconch is coiled heterostrophically (Mathildidae, Fig. 15.182A) or anastrophically (Architectonicidae) – according to Robertson (1985b) and Bieler (1993) anastrophy can be considered as an extreme expression of heterostrophy. Typically the operculum is thin, corneous and spiral, but in many architectonicids the operculum takes the form of a solid, spirally grooved cone. Architectonicoideans have a broad foot featuring a pair of antero-lateral processes and anterior and posterior glands. The head bears a pair of well-developed tentacles, with an eye situated near the base of each tentacle (Climo 1975; Haszprunar 1985e, 1985f; Bieler 1993).

Much of the information in this account derives from studies by Robertson (1964, 1967, 1970a, 1970b, 1973a, 1985b, 1989), Robertson, Scheltema & Adams (1970), Climo (1975), Haszprunar (1985b, 1985d, 1985e, 1985f, 1988a) and Bieler (1988, 1993). Architectonicoideans feed on cnidarians, and the gut shows the following specialisations: the proboscis is highly extensile and eversible; the radula is usually modified taenioglossate with five teeth per row or modified ptenoglossate featuring numerous marginal teeth (Figs 15.182F; 15.183I); the jaws are long and narrow; and the oesophagus and often the buccal cavity are cuticularised (Robertson 1973a; Haszprunar 1985e, 1985f; Bieler 1988, 1993). The gills are not true ctenidia, but of secondary origin (Fig. 15.182D; Haszprunar 1985e, 1985f). Other organs of the mantle cavity include the elongate

osphradium, ciliated dorsal and ventral ridges, hypobranchial and pigmented mantle glands and the large kidney (Fig. 15.182D; Robertson 1973a; Haszprunar 1985e, 1985f; Bieler 1993).

The tentacles are short (Fig. 15.182C), and the eyes, on the outer sides of the tentacular bases, are equipped with a large lens. The nervous system is streptoneurous with long pleuropedal connectives (the epiathroid condition), and with three ganglia associated with the visceral loop (for details and further discussion see Haszprunar 1985e, 1985f; Huber 1993). The structure of the sense organs and nervous system follows the same pattern in the Mathildidae and Architectonicidae (Haszprunar 1985b, 1985d).

Modes of reproduction vary widely within both families, from gonochorism through protandry to simultaneous hermaphroditism. All species lack a penis, sperm transfer being effected probably via spermatophores, as demonstrated for some architectonicids by Robertson (1989). Eggs connected by chalazae (tubular extensions of the egg capsule), are deposited in variously shaped gelatinous masses on the host cnidarian or within the shell umbilicus (Figs 15.182G, H; 15.183G, H; Robertson 1967; Robertson *et al.* 1970; Climo 1975).

After hatching, architectonicid veligers may spend considerable time within the plankton before entering into a benthic, post-larval phase during which a suitable host is sought and high mortalities are sustained (Robertson *et al.* 1970). The biology of larval mathildids presumably follows a similar pattern, although some species may be direct developers.

As far as is known, all architectonicoideans are ectoparasites of colonial cnidarians (chiefly zoantharian, scleractinian and antipatharian corals) (Robertson 1967, 1970b; Climo 1975). Host specificity combined with chance settlement of post-larvae near suitable hosts appear to be the major factors limiting distribution (Robertson 1964; Robertson *et al.* 1970).

The Architectonicoidea are of special phylogenetic and systematic interest since, like the Pyramidelloidea, the group is seen, in a phenetic sense, to occupy an intermediate position between the prosobranch Caenogastropoda on the one hand and the classically defined Opisthobranchia on the other (Robertson 1973a, 1985b; Haszprunar 1985b, 1985d, 1985e, 1985f, 1988a). As Bieler (1988) has remarked, excessive emphasis on the 'ptenoglossate-like' radula of *Architectonica*, which was incorrectly thought by some (for example, Troschel 1875) to be similar to the true ptenoglossate radula, has led to an erroneous association of this family and the Mathildidae with caenogastropod groups such as the Janthinoidea and Triphoroidea. Ultrastructural studies of the osphradium (Haszprunar 1985b) and spermatozoa (Healy 1982a, 1988a, 1991, 1993a; Healy & Jamieson 1991), as well as detailed analyses of anatomy and radular morphology (Haszprunar 1985b, 1985d; Bieler 1988) have established beyond question that the Architectonicoidea should be incorporated in the Heterobranchia. Anatomically, the Mathildidae are considered to be more primitive than the Architectonicidae although the two families share a number of specialised features (see Haszprunar 1985e, 1985f).

Architectonicidae are recorded from all states and the Northern Territory, occurring both intertidally and offshore in shallow to moderately deep water (20–150 m, occasionally to 750 m) (Garrard 1977; Bieler 1993). Mathildidae prefer deep water (100–1000 m), but have recently been recorded in shallow water from the Coral Sea (I. Loch personal communication). To date Australian mathildids have been recorded only from the east coast.

Family Mathildidae

Mathildids are shallow to deep-water architectonicoideans distinguishable from architectonicids chiefly by the moderately small, turreted, highly sculptured shell (umbilicus absent or narrow) and an operculum which lacks an internal peg (Fig. 15.182A, B, E).

The first Australian species in the family to be described was *Mathilda elegantula* (= *Eucharilda elegantula*) from Port Jackson, New South Wales by Angas in 1871. Hedley (1901, 1903) added

two further species and later Iredale (1929b) introduced the genera *Opimilda*, *Mathildona*, *Eucharilda* and *Charilda*. Laseron (1951b) presented an updated listing of New South Wales mathildids, including descriptions of five new species and a brief commentary on all of Iredale's genera. A number of species recognised by Laseron (1951b) have subsequently been shown to belong to caenogastropod families such as the Triphoridae, Cerithiidae, Eulimidae and possibly the Cerithiopsidae. The Mathildidae of Australia have not been reviewed or examined anatomically and presently it is impossible to estimate the number of species from the region. The absence of a generic review of the family leaves the status and endemism of all genera open to question (Bieler 1995). Bieler, referring to his review of the Mathildidae from New Caledonia and the Loyalty Islands (see Bieler 1995), advised that 'not even the shell characters support traditional generic boundaries' within the Mathildidae. He demonstrated that *Opimilda* is a synonym of *Mathildona*, and remarked that 'the distinction between *Opimilda* and *Mathilda*, as currently defined, is nebulous'. Although the status of many mathildid genera will undoubtedly change when reviews are published, no attempt is made in the present work to synonymise these taxa. It should be noted, however, that the type species of *Charilda*, *Mathilda rosae* belongs to the Eulimidae (Bieler 1995). When large scale benthic sampling of the continental shelf is carried out, it is inevitable that range extensions and new species will result.

Shells of most Australian species are typically 'mathildid' in character, being tall-spined with cancellate sculpture (Fig. 15.182A, B). The majority are small, 2–7 mm in length, but *Opimilda decorata* and *Eucharilda elegantula* reach 15–20 mm in length.

Presence of a well-developed foot at first suggests that mathildids are highly mobile. However, this may not follow automatically, as, like architectonicids, they apparently live attached by mucus to host corals (Climo 1975).

Only two mathildid species have been examined anatomically: *Gegania valkyrie* and *Fimbriatella maoria* (Climo 1975; Haszprunar 1985f). The cuticularised lining of the buccal cavity and oesophagus, the morphology of the radula (Fig. 15.182F) and proboscis, and a demonstrated association with black coral (Climo 1975; Haszprunar 1985e, 1985f) suggests that mathildids, like architectonicids, feed on cnidarians. Whether mathildids show host specificity remains to be determined. Mathildids have a small, bilamellate osphradium which contrasts with the larger, unilamellate osphradium of architectonicids (Fig. 15.182D; Haszprunar 1985f).

Haszprunar (1985f) has described in detail the circulatory system of the New Zealand species *Gegania valkyrie*. The heart lies on the left side of the mantle roof and is partly overlain by the kidney. Blood returning from the visceral and head-foot regions, drains first into a peri-oesophageal sinus and then into a muscular vesicle (possibly an accessory heart) in the floor of the mantle cavity. Subsequently the blood is oxygenated through close contact with epithelia of the mantle roof, kidney and gill lamellae. Gas exchange in mathildids occurs chiefly across the epithelia of the kidney and mantle roof and not the gill lamellae (Haszprunar 1985f).

Fimbriatella maoria and *Gegania valkyrie* are typical of lower heterobranchs in having a large kidney in the mantle roof, bordered on the right by the rectum and genital ducts, and on the left by dorsal ciliary tracts (Fig. 15.182D; Haszprunar 1985f). In *Gegania valkyrie*, two sets of secondary gill lamellae are present – one between the oviduct and kidney and the other near the pericardium (Fig. 15.182D; Haszprunar 1985f). Lamellae are absent in *Fimbriatella maoria* (Haszprunar 1985f, as *Opimilda maoria*). Sense organs (Fig. 15.182C) and the nervous system are as described for the superfamily.

Haszprunar (1985f) suggested that sperm transfer in mathildids probably involves spermatophores as in the Architectonicidae and Pyramidelloidea (Robertson 1978, 1989). Sperm ultrastructure of mathildids clearly indicates a close relationship with the

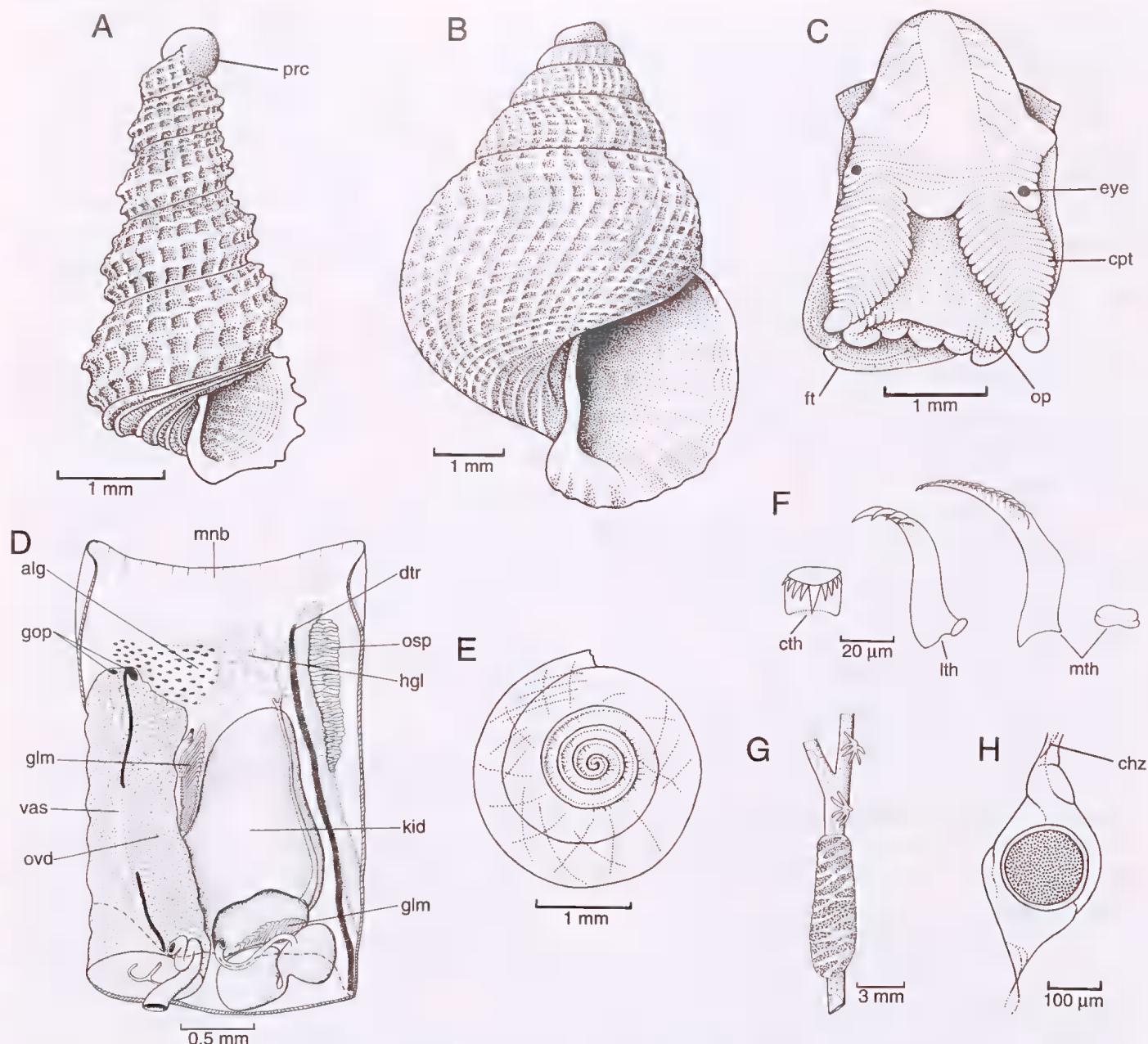


Figure 15.182 Family Mathildidae. A, *Opimilda decorata*, shell, apertural view showing hyperstrophic protoconch. B–H, *Gegania valkyrie*: B, shell, apertural view; C, head and foot of preserved specimen (the ridges on the cephalic tentacles are probably an artefact of preservation); D, organs on the roof of the mantle cavity; E, operculum, inner surface; F, half a radular tooth row; G, egg mass, containing strap-like deposits of eggs, wrapped around antipatharian coral *Parantipathes tenuispina* (Fig. 15.182G). H, detail of egg capsule and chalazae. alg, anal gland; chz, chalazae; cpt, cephalic tentacle; cth, central tooth; dtr, dorsal ciliary tract; eye, eye; ft, foot; glm, gill lamellae; gop, gonopores; hgl, hypobranchial gland; kid, kidney; klo, kidney opening; lth, lateral tooth; mgl, mucous gland; mnb, mantle border; mth, marginal teeth; op, operculum; osp, osphradium; ovd, oviduct; pcd, pericardium; pre, protoconch; spl, spermatolytic gland; sr, seminal receptacle; vas, vas deferens. (A, after Hedley 1903; B, C, E, G, H, after Climo 1975; D, after Haszprunar 1985f; F, after Bieler 1988)

Architectonicidae (Healy 1995). Climo (1975) has shown that egg masses of *Gegania valkyrie* contain strap-like rows of embryos wrapped around the stem of the antipatharian coral *Parantipathes tenuispina* (Fig. 15.182G). Egg capsules of this species are linked by chalazae and embedded in a gelatinous substance (Fig. 15.182G, H).

Like Architectonicidae, most mathildids probably have a planktonic veliger stage judging by their protoconch morphology. Ponder (1985a) suggested that direct development may occur in the New Zealand species *Brookesena neozelanica* as its protoconch is paucispiral with a bulbous initial whorl (characters associated with direct development).

Mathildidae have a worldwide distribution, but appear to be more prevalent in temperate waters. Seven species were listed by Iredale & McMichael (1962) from New South Wales, one of which, *Opimilda decorata* (Fig. 15.182A), also occurs in Tasmania (May 1923) and has a subspecies (*O. decorata*

aupouira) in northern New Zealand. Two species were listed by Hedley (1910b) from Queensland. The absence of published records from other Australian states probably reflects a lack of adequate deep-water sampling in these regions as well as the scarcity and small size of mathildids. The genus *Glyptozaria* which has been placed in the Turritellidae (Iredale & McMichael 1962; Garrard 1972) and associated with the Pyramidellidae (together with other mathildids) by Laserson (1951b), has been demonstrated by Houbbrick (1981d) to belong to the Cerithiidae (see also Bieler 1995 for further discussion).

There are no published records of fossil Mathildidae from Australia.

Study of live mathildids will always be difficult because of their small size and scarcity. Nonetheless, much valuable information has been gleaned from preserved material, including the basic anatomy of the family and aspects of reproduction (see Climo 1975; Haszprunar 1985f) including sperm ultrastructure (Healy unpublished data).

Family Architectonicidae

Architectonicids live in shallow to deep-water. They have low-spired, discoidal or turbinate shells, almost smooth or variously sculptured with spiral grooves, ridges and granulations (Fig. 15.183A). The umbilicus is typically wide, and sealed apically with the downward-pointing (anastrophically coiled) protoconch. The inner side of the operculum always bears a small peg (Fig. 15.183C, D).

Prior to Garrard's (1977) review, the Australian Architectonicidae had only received attention in checklists and popular books, or in occasional species descriptions (for chief references see Iredale & McMichael 1962; Garrard 1977). Most of the taxa described by Iredale have been relegated to synonymy except for a few species in the genus *Solatisonax* and two subgenera of *Heliacus* (*Torinista*, *Grandeliacus*) (see Bieler 1986, 1993 for discussion). Recently, Bieler (1993) published a detailed monograph on the extant Architectonicidae from the Indo-Pacific. Of the 88 valid species recognised by Bieler from the region, 59 are recorded from Australia (a few of these records are regarded by Bieler as in need of verification). According to Bieler, all the Indo-Pacific architectonicid genera occur in Australian waters, and none can be considered endemic to Australia. Particularly well represented are the genera *Architectonica* (nine species), *Heliacus* (17 species, 10 of

which are in the subgenus *Torinista*) and *Pseudotorinia* (six species). Only four species appear to be restricted either entirely or largely to the Australian region: *Architectonica grandiosa*, *Philippia lutea* (also occurring in New Zealand) *Pseudotorinia colmani* and *Solatisonax injussa*. Australian fossil architectonicids have been described by Tenison Woods (1879), Chapman (1912), Finlay (1927b), Chapple (1941), Buonaiuto (1975) and Garrard (1977).

External features (Fig. 15.183B, F) are as described for the superfamily. The operculum may be round or oval and thin (for example, *Architectonica*, *Philippia*; Fig. 15.183A, C, D) or tall, solid and conical (for example, *Granosolarium*, *Heliacus*; Fig. 15.183B, F). External animal colour varies from white to pink in *Architectonica* and *Philippia*, and from brown to green-black in *Heliacus*.

Proboscis and buccal modifications are as outlined for the superfamily. In most genera the radula has a strongly cuspidate central tooth and variable number of curved, cuspidate marginals (Fig. 15.183I). Some species of *Architectonica* lack a central tooth, and in *Discotectonica* and *Granosolarium*, a cuticularised, toothed rod-like structure of uncertain homology either takes the place of the radula (Boss & Merrill 1984; Haszprunar 1985e; Bieler 1988, 1993) or accompanies it (*D. disca* – see Boss & Merrill 1984). Boss & Merrill (1984) have used radular features to

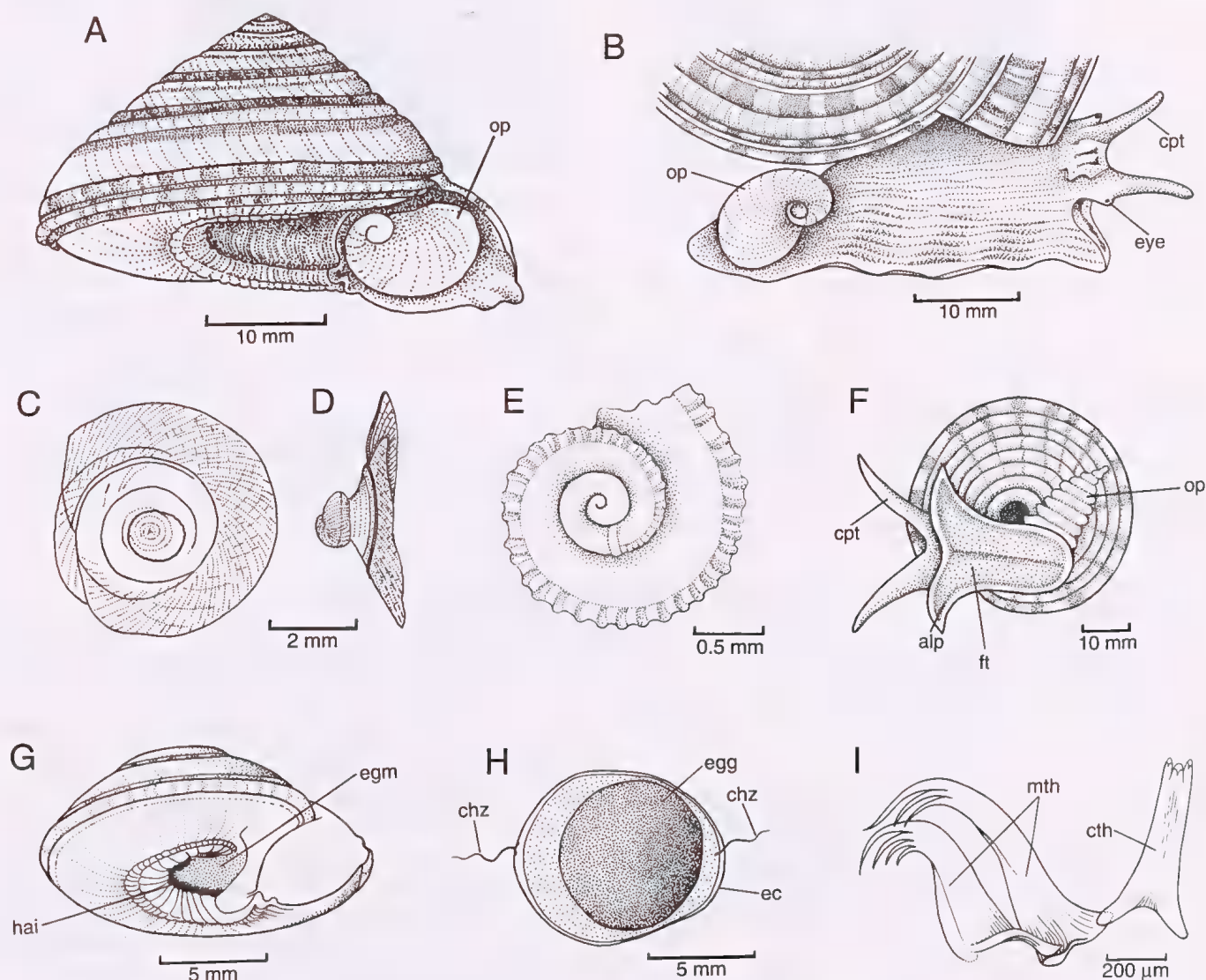


Figure 15.183 Family Architectonicidae. A, B, *Architectonica perspectiva*: A, shell, apertural view, operculum closing the aperture; B, head and foot of crawling animal. C, D, *Philippia radiata*, operculum: C, outer surface; D, lateral view, showing the internal peg. E, *Pseudomalaxis theditis*, shell, ventral view. F, *Heliacus variegatus*, underside of crawling animal, showing antero-lateral processes of the foot and conical operculum. G, H, *Philippia radiata*: G, egg mass deposited within shell umbilicus; H, egg capsule and chalazae which links eggs together in the egg mass. I, *Philippia oxytropis*, central tooth and marginal teeth. alp, antero-lateral process of foot; chz, chalazae; cpt, cephalic tentacle; eth, central tooth; ec, egg capsule; egg, egg; egm, egg mass; eye, eye; ft, foot; hai, hairs of periostracum; mth, marginal teeth; op, operculum. (A, after Hedley 1903; B, after Kiener 1838–1839; C, D, G, H, after Robertson 1970a; E, after Garrard 1977; F, after Quoy & Gaimard 1830–1834; I, after Climo 1975)

[S. Weidland]

15. PROSOBRANCHS

subdivide the Architectonicidae into three subfamilies, a decision rejected by Bieler (1986), but supported by available sperm data (Healy 1993a, 1995). Robertson (1967) noted that in the laboratory, *Heliacus* (*H. cylindricus* and *H. trochoides*) feed only at night, leaving 3–4 mm deep holes in the flesh of *Palythoa* colonies. The question remains as to what type of cnidarians larger architectonicids such as *Architectonica perspectiva* and *A. maxima* feed on. Various groups have been suggested such as pennatulids and sand anemones (Abbott, R.T. 1974; Garrard 1977). Bandel (1976a) noted that the Atlantic species, *A. nobilis*, emerges from the sand at dawn or night (rarely during day light) to feed on 'all kinds of soft-bodied actinian-type coelenterates'.

Circulation, excretion, sense organs and the nervous system essentially are as described for the Mathildidae and the superfamily (see also Huber 1993). The architectonicid osphradium is unilamellate and is described in detail by Haszprunar (1985b, 1985e). As in all heterobranchs, ctenidia are absent. Instead, epithelial extensions of the hypobranchial gland form secondary gill lamellae (Haszprunar 1985e). The pallial kidney and mantle roof epithelium are probably the chief sites of gas exchange (Haszprunar 1985e).

Architectonicids display many reproductive modes from gonochorism (*Philippia*, *Granosolarium*) through protandry (*Heliacus*) to simultaneous hermaphroditism (*Heliacus*, *Architectonica*) (Robertson 1973a, 1985b; Haszprunar 1985e; Bieler 1988). Healy (1982a, 1988a, 1991, 1993a) and Healy & Jamieson (1991) have presented ultrastructural studies on spermiogenesis of *Philippia oxytropis*, *Heliacus variegatus*, *Granosolarium* sp. and *Architectonica perspectiva* collected from Queensland. Their work has shown that architectonicids produce a distinctive, modified sperm for internal fertilisation, and that sperm and spermiogenic features support the family's heterobranch affiliation. There is no evidence to endorse Boss' (1982) assertion that architectonicid sperm are dimorphic. Robertson (1989) demonstrated the transference of long (up to 25 mm), dimorphic spermatophores in *Heliacus cylindricus* and *H. perrieri*. Sperm transfer via spermatophores is probably typical for the family.

Deposited eggs of architectonicids, like those of the Mathildidae, are linked by chalazae and embedded in a mass of jelly-like material (Fig. 15.183H; Robertson 1967, 1989; Haszprunar 1985e). In *Heliacus cylindricus*, the egg mass is U-shaped and attached by mucous threads to the host *Palythoa* colony (Robertson 1967). In *Philippia radiata*, eggs are laid within the shell umbilicus (Fig. 15.183G; Robertson 1970a), but in *P. lutea* they are laid as short, orange jelly masses (W.F. Ponder personal communication).

Extended planktonic larval stages (up to six months in the Atlantic *Philippia krebsii* – Robertson *et al.* 1970) may explain the wide distribution of many architectonicid species (Bieler 1986). Newly hatched veligers have two ciliated lobes but this increases to four lobes with age (Haszprunar 1985e). Post-larvae may remain active without feeding for many weeks during which time they must seek out a suitable cnidarian host (Robertson *et al.* 1970).

Architectonicids are rendered difficult subjects for field study by their subtidal preference and generally cryptic nature, burrowing in sand and only emerging at night to feed or spawn or living under rocks or among soft corals (Robertson 1970a; Robertson *et al.* 1970; Bieler 1988). Nonetheless, it is remarkable that the ecology and biology of any species of so widespread a genus as *Architectonica*, has never been examined in detail (see Bieler 1993 for discussion and references).

The unusual shells of architectonicids, often found as beach specimens, are valued as curios by collectors. Bieler (1986) estimates that worldwide, the Architectonicidae comprises about 140 extant species, distributed between eight genera and thirteen subgenera. In Australia, the genera *Architectonica*, *Philippia*, *Pseudotorinia*, *Psilaxis*, and *Heliacus* occur from the intertidal zone (especially *Heliacus*) to moderate depths (100–150 m),

whereas *Solatisonax* and *Discotectonica* species occur down to 750 m (Garrard 1977; Bieler 1993). According to Garrard (1977), of the 41 architectonicid species occurring in Australian waters, only eight are endemic. *Pseudomalaxis* species are known from deep water off New South Wales, Western Australia, Queensland and the Northern Territory (Garrard 1977).

Pseudomalaxis, *Pseudotorinia* and *Heliacus* appear in the Cretaceous followed in the Eocene by *Architectonica* and *Philippia* (see Bieler 1988 p. 227). In Australia, *Pseudomalaxis* is present in the Late Eocene of South Australia (Buonaiuto 1975) and species of *Heliacus* and *Philippia* are recorded from the Miocene of Victoria (Garrard 1977).

Robertson (1967) and Robertson *et al.* (1970) have demonstrated that at least some architectonicids can be studied successfully in the laboratory, particularly species of *Heliacus* and *Philippia*, the cnidarian hosts (zoantharians and scleractinians respectively) of which are known and readily collected. Additional data for the equally common though less accessible genus *Architectonica* are now required (see Bandel 1976a for a brief description of habitat and feeding of *Architectonica nobilis*).

Superfamily RISSOELLOIDEA

This superfamily contains minute marine snails with simple, smooth shells bearing a homeostrophic protoconch. They lack a gill and have a pair of longitudinal, opposed ciliated ridges in the pallial cavity. There is a pigmented mantle gland and the head bears a pair of tentacle-like oral lobes, which, combined with the cephalic tentacles, give the impression of two pairs of head tentacles. The foot has a posterior mucous gland and the kidney lies in the mantle roof. Rissoelloideans are simultaneous hermaphrodites.

The superfamily contains only the Rissoellidae and further details are given in description of the family below.

There has been controversy over the systematic position of the Rissoellidae. They were thought to be related to the Rissoidae until Fretter & Graham (1954) implied that *Rissoella* has opisthobranch rather than prosobranch affinities, although later Fretter (1956) and Fretter & Graham (1962) included *Rissoella* in the Caenogastropoda. Most authors have included them in the Rissooidea, except Nordsieck (1972) who included them in his superfamily 'Microrissoidea' and Golikov & Starobogatov (1975) who erect a new suborder Rissoellina within the Prosobranchia. Ponder (1983b), Haszprunar (1988a) and Ponder & Warén (1988) placed the family Rissoellidae in its own superfamily, the Rissoelloidea, in the Heterobranchia.

Family Rissoellidae

Rissoellid shells are usually less than 5 mm in length and are characteristically smooth, thin and fragile (Fig. 15.184A, B). They are globose to ovate-conic in shape with convex whorls, the last large, the aperture broadly ovate and simple with a thin, sharp peristome. The operculum is semicircular, not spirally coiled, and the marginal nucleus has a short, blunt, internal peg at the apex of the angle on the columellar edge from which run three internal ridges, two parallel to the edge and one at right angles to it (Fig. 15.184C).

The head has long oral lobes that resemble a second pair of tentacles. The cephalic tentacles have the eyes placed in the middle of their bases or well behind on the head (Fig. 15.184F). The foot has well-developed anterior and metapodial glands, the latter capable of producing mucous threads.

The ctenidium is absent, and respiratory currents are largely maintained by a pair of opposed ciliated exhalant ridges which run forward from the anus (Fretter 1948).

Rissoellids feed on diatoms, algal filaments and some detritus (Fretter 1948). Paired jaws are present and the radular teeth show a considerable diversity in shape and cusp pattern depending on

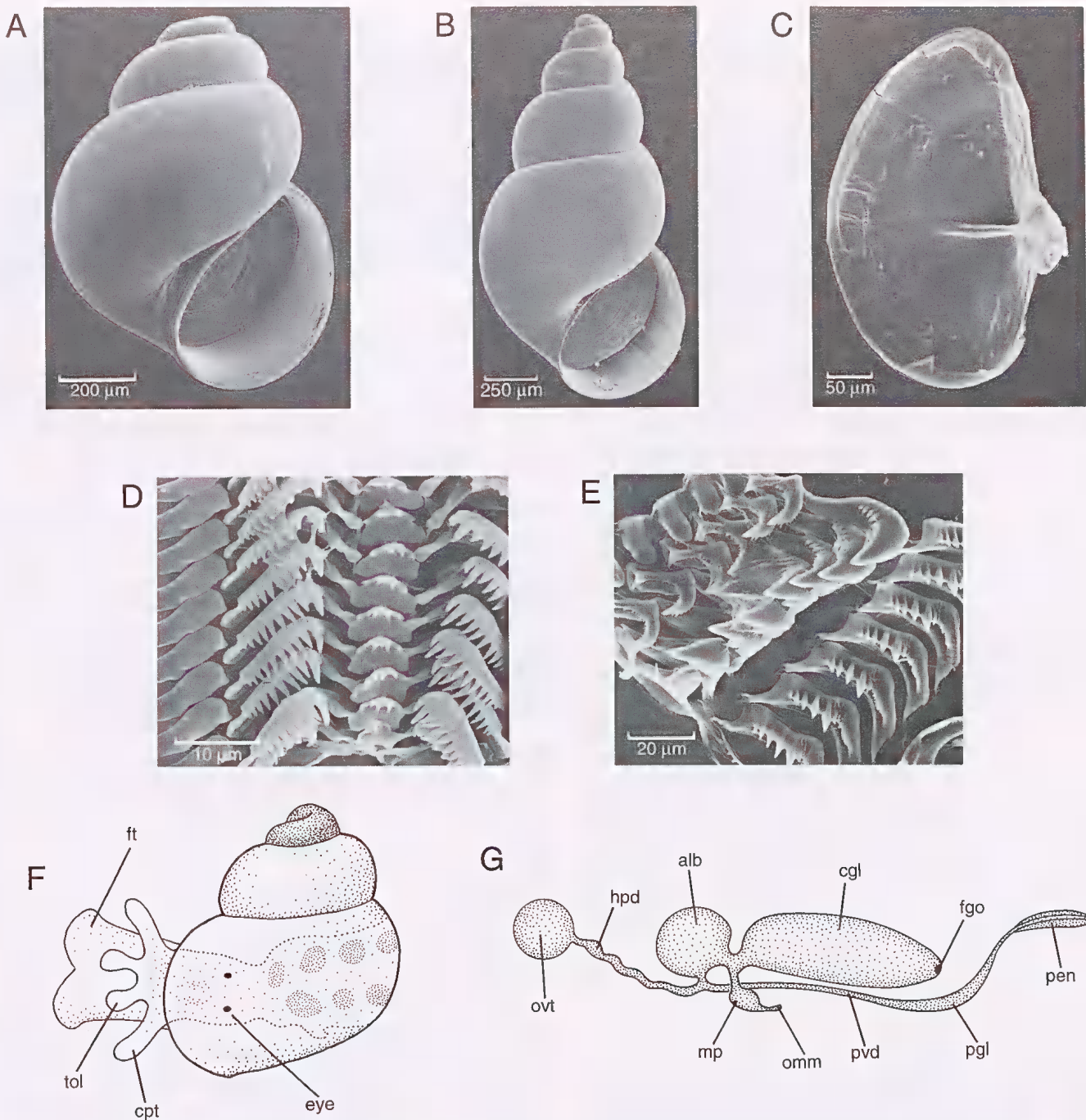


Figure 15.184 Family Rissoellidae. **A, B**, shells, apertural view: **A**, *Rissoella (Rissoella) globosa*; **B**, *Rissoella (Jeffreysiella) secunda*. **C**, *Rissoella (Zelaxitas) micra*, operculum, inner surface. **D, E**, portions of radulae: **D**, *Rissoella (Zelaxitas) micra*, showing central teeth, and lateral and marginal teeth on the left, and lateral teeth on the right; **E**, *Rissoella (Jeffreysiella) secunda*, asymmetrical central teeth, and lateral and marginal teeth on left side. **F**, *Rissoella* sp., animal, dorsal view. **G**, *Rissoella diaphana*, diagram of reproductive system. alb, albumen gland; cgl, capsule gland; cpt, cephalic tentacle; eye, eye; fgo, female genital opening; ft, foot; hpd, hermaphroditic duct; mp, muscular pouch; omm, opening of muscular pouch to mantle cavity; ovt, ovotestis; pen, penis; pgl, prostate gland; pvd, pallial vas deferens; tol, tentacle-like oral lobe. (G, after Fretter & Graham 1962)

the genus group (Fig. 15.184D, E). Central, paired lateral, and zero to two pairs of marginal teeth are present (Ponder & Yoo 1977). The radular teeth are sometimes asymmetrical. There is no crystalline style although there is a gastric shield in the stomach (Fretter 1948).

The kidney is located in the mantle roof and its walls are not folded. The nervous system is concentrated and the visceral loop is drawn forward (Fretter 1948; Huber 1993).

The reproductive systems of two British species were described by Fretter (1948). Both species are simultaneous hermaphrodites with a single gonad (Fig. 15.184G). There is a unique muscular pouch (Fig. 15.184G) of uncertain function, but which may be used to clear waste material from the genital duct. The pallial oviduct consists of a posterior albumen gland and an anterior capsule gland, the former probably the site of fertilisation, since spermatozoa are frequently found there during the breeding

season (Fretter 1948). The capsule gland has thin, ciliated ventral and anterior walls and has two openings, one to the exterior and the other to the muscular pouch. The vas deferens runs forwards beneath the pallial oviduct, becoming glandular (prostate gland) towards the mouth of the mantle cavity, and passes up the right side of the head and through the penis to its tip. The external penis is relatively short and tubular and usually lies folded back along a groove in the body wall.

The egg capsules of only two (European) species of *Rissoella* are known. They are hemispherical and attached by the flattened base to weed; each capsule contains one to three eggs. The eggs have a supply of albumen; each has its own covering and is suspended in a fluid which fills the capsule. There is an intracapsular veliger stage and the young emerge from the capsule at the crawling stage (Fretter 1948). Some species are annuals and, at least in Europe, few adults survive the winter.

15. PROSOBRANCHS

Rissoellids occur in the lower littoral and shallow sublittoral throughout the world, including Antarctic, Subarctic and Subantarctic seas, and are often found in rock pools associated with algae.

Thiele (1929–1935) described the radula of several rissoellids and, because they showed very different morphology, introduced new genus-group taxa. Robertson (1961) listed the taxa included in the family. Only one Australasian species had been recognised at the time of publication from Robertson's list, but Ponder (1966b, 1968c) included in the group several New Zealand species that had previously been placed in the Rissoidae and Littorinidae. Ponder & Yoo (1977) revised the Australian species and reviewed the genus-group taxa, recognising one genus containing five subgenera (one of which is not known in Australia) separated mainly on radular characters. There is now evidence that considerable anatomical differentiation occurs between at least two of these 'subgenera' so that generic differentiation may be required (Haszprunar 1988a).

The family contains less than 30 named species, currently included in the genus *Rissoella* which is divided into five 'subgenera' based primarily on radular morphology (Ponder & Yoo 1977). In Australia, there are 14 species and subspecies currently classified in four subgenera (Ponder & Yoo 1977). *Rissoella sensu stricto* and *R. (Jeffreysilla)* have a worldwide, cool temperate to tropical distribution, *R. (Zelaxitas)* is confined to New Zealand and southern Australia, and *R. (Jeffreysiella)* is confined to Australia, New Zealand, the South Pacific, the Subantarctic and the Antarctic. There are four Australian species of *R. (Rissoella)*, all of which have rather globose shells. *Rissoella (Jeffreysilla)* also contains species with globose shells which have a small to large umbilicus, there being one species with three subspecies in Australia. Species of *R. (Zelaxitas)* are characterised by their short-spined, globose, brown shells and distinctive radula, there being two Australian species. Species of *R. (Jeffreysiella)*, among which are four Australian species and two subspecies, are distinctive in generally having tall-spined shells with a somewhat offset protoconch, and in having seven teeth instead of five in each row of the radula. Several additional, unnamed rissoellid species are known from Australia (W.F. Ponder personal observation).

There is no reliable fossil record of rissoellids, presumably because their fragile shells are easily crushed or dissolved.

Superfamily OMALOGYROIDEA

Omalogyroideans are minute marine snails with discoidal shells. They are hermaphrodite and characterised by having a simple alimentary canal, including a reduced radula, a hermaphroditic reproductive system with separate gonads and no true penis (the penis is an extension of the bursa copulatrix), a pallial kidney, no gill and a reduced osphradium. They do not have a pallial tentacle, and the jaw is small and simple. This superfamily currently comprises a single family, Omalogyridae.

Subsequent to the anatomical work of Vayssi re (1895) and Fretter (1948) on European species, little was done to elucidate the taxonomic position of this group until Healy's (1988a) investigation of the sperm quite recently. Haszprunar (1985d, 1988a) and Healy (1988a) discussed the systematic position of the Omalogyridae and included them in the Heterobranchia. Despite a suggestion by Fretter (1948) and Fretter & Graham (1962) that the group might have opisthobranch affinities, most authors had, until the mid 1980s, included this group in the Rissooidea.

As only one family is included currently in the superfamily, further details are given in the family description.

Family Omalogyridae

Omalogyrids are some of the smallest molluscs. Their shells are minute (usually less than 2 mm in diameter and some less than 0.5 mm), planispiral, usually reddish or brown in colour, often

thin, and with rounded whorls (Fig. 15.185A, B). The shell surface may be smooth or sculptured with crenulated axial ridges, and the homeostrophic protoconch is often sculptured. The spire is depressed, the aperture rounded and simple, and the sutures deep. The base has a broad, shallow umbilicus. The operculum has a central nucleus, is corneous and has only a few whorls (Sleurs 1984, 1985).

The cephalic tentacles are short and lobe-like (*Omalogyra* species; Fig. 15.185D) or short and slender (*Ammonicera* species; Fig. 15.185C) and have prominent eyes in the middle of their bases. The snout is short and bifid. The foot is short and oblong anteriorly and rounded posteriorly. The posterior pedal gland is well developed with a longitudinal groove, and can produce long mucous threads that help the animal to maintain its hold or allow it to hang from surface film.

There are opposed ciliated ridges on the left side of the pallial cavity, an inconspicuous osphradium and no gill (Haszprunar 1988a). A conspicuous pigmented (usually black) mantle organ lies in the middle part of the pallial roof.

Omalogyra species feed on the cell contents of algae such as *Ulva*, using the stiletto-like radular teeth (Fig. 15.185E) to puncture the cell walls (Fretter 1948). There are no jaws and the radula has one to four teeth in each row (Sleurs 1984, 1985a, 1985b). The following anatomical information is from Fretter (1948) and is based on the European *Omalogyra atomus*, the type species of *Omalogyra*. The oesophagus is simple and the stomach is relatively small and lacks a crystalline style. The intestine is a short, straight tube that runs along the right side of the genital duct.

Omalogyra atomus is protandrous, but is also a simultaneous hermaphrodite in that both gonads are ripe together for much of the time. The gonad consists of a separate ovary and testis (Fig. 15.185F), and there is a single genital opening near the mouth of the mantle cavity on the right side. The sperm morphology is similar to that of other heterobranchs (Healy 1988a). There is a muscular sac which is connected to the posterior end of the prostate gland and the penis is a whip-like, muscular retractile tube lying within the lumen of the prostate gland and anterior part of the reproductive system (see Fig. 15.185F). It is formed as an extension of the bursa copulatrix and is therefore not a true penis. *Omalogyra atomus* is an annual and only juveniles survive the winter. The female reproductive glands mature in the summer and the male system degenerates. It is probable that individuals that hatch in the summer practise self fertilisation as they do not develop male copulatory organs, although the testis contains mature sperm (Fretter 1948). Egg capsules are spherical or ovoid, slightly flattened along the basal surface and are attached to algal fronds. Each capsule contains one egg (rarely two) embedded in albumen and the larva passes through the veliger stage within the capsule (Fretter 1948).

The small kidney has simple walls and lies in the mantle roof. Huber (1993) provided information on the nervous system of European taxa showing that both the cerebral and pedal ganglia are fused.

Omalogyrids are found worldwide, usually in the lower intertidal and sublittoral zones, living on algae. Several species occur in Australia, but only two are named. Both were described by Laseron (1954a) and placed in his genus *Helisalia* – this is probably a synonym of *Omalogyra* (W.F. Ponder personal observation). *Omalogyra liliputia* is common on intertidal algae in New South Wales and has a maximum shell diameter of about 0.5 mm (Laseron 1954a). The other species, *H. sucina*, is a species of *Ammonicera*. A third species included by Laseron in *Helisalia*, *H. pallida*, is an orbitestellid (*Microdiscula*) (Ponder 1990b). Sleurs (1984, 1985) has described several omalogyrid species from Papua New Guinea and some of these may be conspecific with some of the several species collected from tropical Australia.

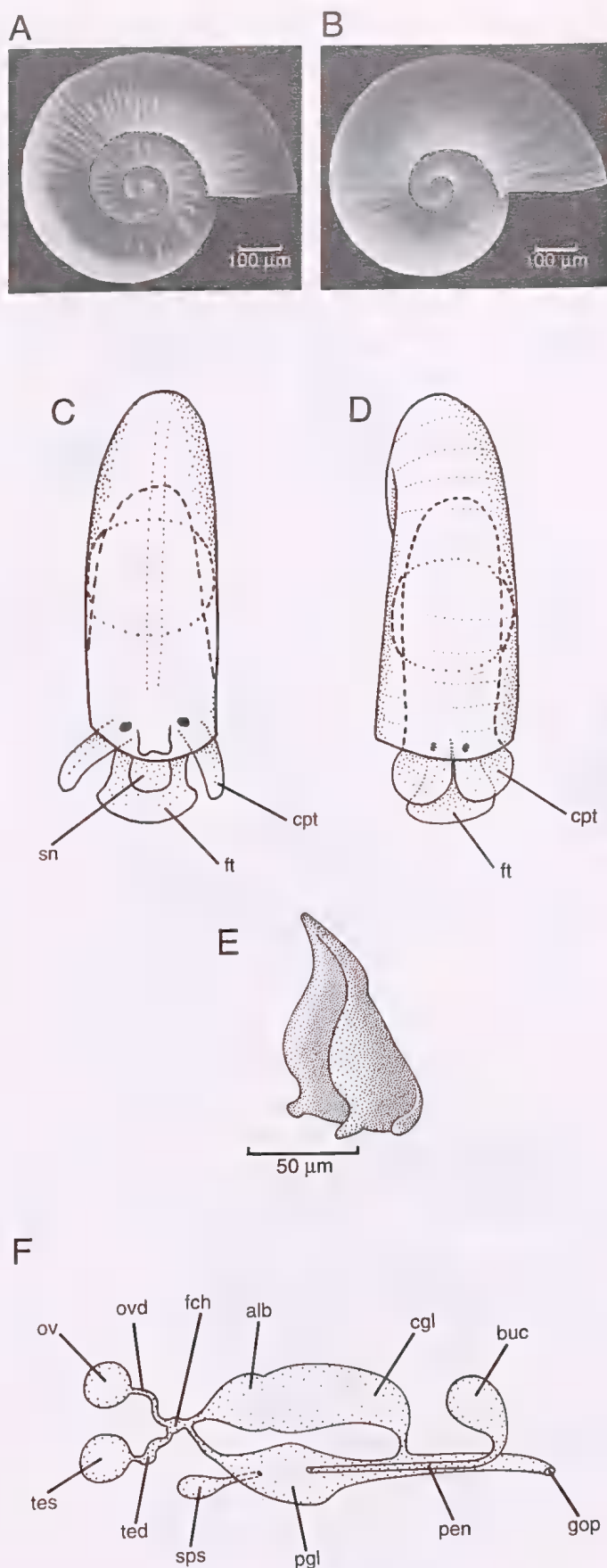


Figure 15.185 Family Omalogyridae. A, B, shells, apical view: A, *Ammonicera sucina*; B, *Omalogyra liliputia*. C, D, live animals, dorsal view: C, *Ammonicera sucina*; D, *Omalogyra liliputia*. E, *Omalogyra* sp., central tooth of radula. F, *Omalogyra atomus*, diagram of reproductive system. alb, albumen gland; buc, bursa copulatrix; cgl, capsule gland; cpt, cephalic tentacle; fch, fertilisation chamber; ft, foot; gop, genital opening; ov, ovary; ovd, ovarian duct; pen, penis; pgl, prostate gland; sn, snout; sps, sperm sac; ted, testis duct acting as seminal vesicle; tes, testis. (E, after Vayssi re 1895; F, after Fretter & Graham 1962)

[A, B, W.F. Ponder; C, D, S. Weidland; E, F, C. Eadie]

The earliest fossil omalogyrids are from the Eocene of Europe (Lozouet & Maestrati 1982). Bandel (1988) discussed the similarities of omalogyrids to some Mesozoic taxa previously grouped in the Euomphaloidea.

Superfamily PYRAMIDELLOIDEA

The Pyramidelloidea is a large and diverse worldwide superfamily of marine ectoparasitic snails. Pyramidelloidean shells range from almost needle-like to flat-spined, from multiwhorled to limpet-like, and have an often markedly heterostrophic protoconch and simple aperture lacking an anterior canal. An operculum with an excentric nucleus is usually present. The head bears rabbit ear-shaped tentacles with the eyes on their inner bases and a snout-like mentum (propodium) above which the mouth opens between the tentacular bases. The foot has a rather short creeping sole or (in the Amathinidae) has the metapodium modified to form a sucker. The anterior alimentary canal is complex, forming an acrembolic proboscis, with the buccal cavity modified to form a pump. There is no radula, and the jaws either form a piercing stylet, as in the Pyramidellidae, or are lost. The stomach is a simple sac into which the digestive gland opens.

Pyramidelloideans are almost certainly all ectoparasites, and feed on a wide variety of invertebrate hosts. The ctenidium is absent (as in all heterobranchs) and in a few larger species a secondary gill is formed. There is a conspicuous pallial gland and the osphradium is very inconspicuous. A pair of opposed ciliated ridges in the pallial cavity extend posteriorly to a short caecum. They are hermaphrodites, with a partly pallial reproductive system and an invaginable penis. Both direct and planktonic larval development are found in the group.

Pyramidelloidean fossils are known from the Palaeozoic but the family assignment of fossil groups is unsettled.

This group, like most of the Heterostropho, was classified with the 'prosobranchs' in the 'mesogastropods'. The anatomical work of Fretter & Graham (1949) showed the Pyramidellidae to be similar to opisthobranchs in many characters, but controversy as to their systematic position continued until recently (see under Pyramidellidae for more details). Until recently, only two families were included in the superfamily. Since this section on Pyramidelloidea was written, however, War n (1993) has introduced the Cimidae and Bandel (1996) has proposed Ebalidae and Donaldinidae. The latter families include species (including some from Australia) previously included in the Pyramidellidae whereas the Cimidae contains undescribed Australian species (A. War n & W.F. Ponder personal observation). The relationships of these recently proposed families to Pyramidellidae and other lower heterobranchs have yet to be determined.

Family Pyramidellidae

Pyramidellids are marine ectoparasitic snails with planispiral to elongate shells which usually bear a distinctly heterostrophic protoconch and often have one or more columellar plaits (Fig. 15.186A–F). The head-foot has short, rabbit ear-shaped tentacles with eyes on their inner sides, and a snout-like mentum (Fig. 15.186G). A pigmented mantle organ is present and a secondary gill is only rarely present. They have no radula, but have a piercing stylet and a buccal bulb and pump associated with a proboscis which they use to feed on the body fluids of various invertebrates (Fig. 15.186H). The anterior alimentary canal is greatly elongated and the stomach is minute. The salivary glands are long and tubular. A gill, when present, is situated on the right of the dorsal ciliated ridge in the pallial cavity.

Earlier workers, including Thiele (1929–1935) and Wenz (1940a), considered pyramidellids to be related to the caenogastropod family, Eulimidae. Kosuge (1966a) and some subsequent writers including Boss (1982), placed both families in the Heterogastropoda, a heterogeneous group (see Haszprunar 1985d) containing both caenogastropods and heterobranchs.

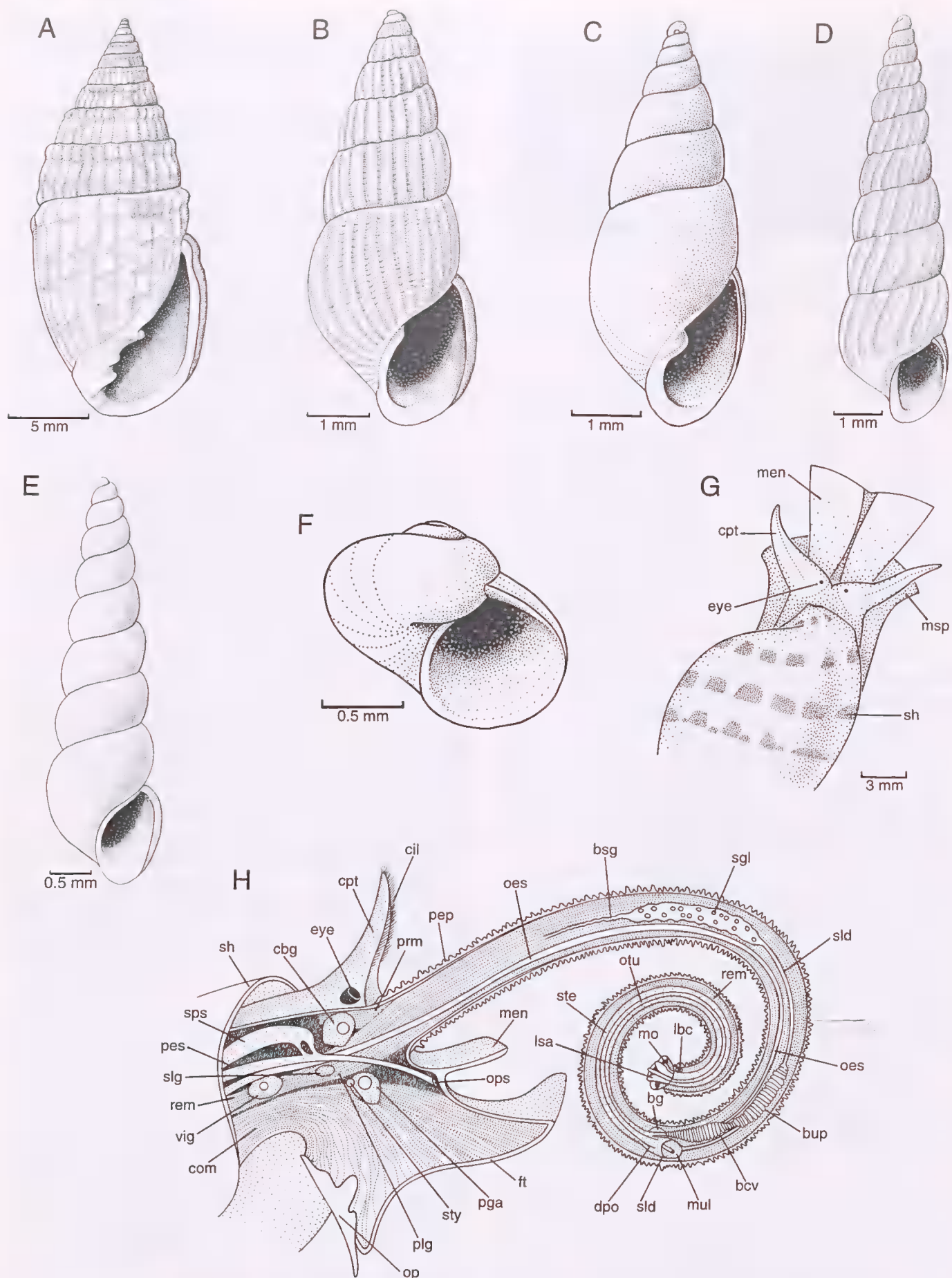


Figure 15.186 Family Pyramidellidae. A–F, shells, apertural view: A, *Otopleura auriscati*; B, *Linopyrga pascoei*; C, *Odostomia angasi*; D, *Chemnitzia mariae*; E, *Koolonella moniliformis*; F, *Pseudoskenella depressa*. G, *Pyramidella acus*, head and foot. H, *Odostomia unidentata*, the anterior gut, diagrammatic lateral view, with proboscis extended. bcv, buccal cavity; bg, buccal ganglion; bsg, bladder of salivary gland; bup, buccal pump; cbg, cerebral ganglion; cil, cilia; com, columellar muscles; cpt, cephalic tentacle; dpo, dorsal pouch of buccal cavity; eye, eye; ft, foot; lbc, labial commissure; lsa, lip of stylet aperture; men, mentum; mo, mouth; msp, mesopodium; mul, muscles moving stylet; oes, oesophagus; op, operculum; ops, opening of penial sheath; otu, oral tube; pep, papilla on epithelium of the proboscis; pes, penial sheath; pga, pedal ganglion; plg, pleural ganglion; prm, protractor muscles of the proboscis; rem, retractor muscle; sgl, salivary gland; sh, shell; sld, salivary duct; slg, suboesophageal ganglion; sps, sperm sheath; sty, statocyst; ste, stylet in stylet tube; vig, visceral ganglion. (G, after Ponder 1988; H, after Fretter & Graham 1949)

[A–F, S. Weidland; G, H, C. Eadie]

Fretter & Graham (1949) suggested that pyramidellids are actually opisthobranchs and this idea gained some acceptance, although some workers (for example, Gosliner 1981; Robertson 1985b) rejected this placement. Data from sperm morphology (see Healy 1988a for summary) and osphradial structure (Haszprunar 1985b) provide additional strong evidence of heterobranch affinities of Pyramidellidae. Since this text was written Wise (1996) has published an important paper on the phylogeny and anatomy of pyramidellids; his work is not discussed here.

Shells are usually small, some up to 20 mm in length and typically elongate, although a few species are trochiform to planispiral (Fig. 15.186A–F). The protoconch is smooth, heterostrophic, helical or planorbid, multispiral or, more rarely, paucispiral. The teleoconch surface varies from smooth to ribbed, the sculpture is spiral, axial, or a combination of both. The aperture is of variable shape, lacks an anterior siphonal canal and usually lacks a varix. The columella is smooth or has one to three folds. The operculum is horny, thin and paucispiral and sometimes bears a peg on its inner surface.

The foot is short, broad anteriorly, tapered posteriorly and has a ciliated, creeping sole sometimes with a posterior pedal gland. There is a well-developed snout-like mentum (modified propodium) above which lies the rhynchostome (*ie.* the opening to the introvert) between the tentacular bases. The cephalic tentacles have concave outer surfaces; the concavities are lined with strong cilia. These tentacles are richly supplied with nerves and may be important in sampling the water in search of prey (Fretter & Graham 1949). The eyes are close together on the inner sides of the tentacles.

The mantle cavity usually has no gill, but has an inconspicuous osphradium, a conspicuous hypobranchial gland, and a pigmented mantle organ (Robertson 1985b); its colouration is often diagnostic for species. A secondary gill is present in species of *Pyramidella* (Ponder 1987). Two opposed ciliated ridges extend posteriorly into a short caecum, and provide the water circulation in the mantle cavity (Fretter & Graham 1949).

The kidney is small, with unfolded walls and is located in the pallial roof (Fretter & Graham 1949). The auricle is anterior to the ventricle, unlike the situation in opisthobranchs. An aorta forms a conspicuous ridge on the mid dorsal neck.

The nervous system is mainly concentrated into a ring which envelops the proboscis and, in some, the penial sheath. The cerebral ganglia are large, ovate and lie close together, and the visceral nerve loop contains the pedal ganglia, but no parietal ganglia (Huber 1993). The paired statocysts have a single statolith.

Pyramidellids are simultaneous hermaphrodites, the gonad having ripe sperm and ova in the same tubules, although young individuals are usually males until the ova and glandular oviducts are fully developed (Fretter & Graham 1949). They are monaulic and the penis is invaginated and sheathed. The male portion of the gonoduct has a prostate gland close to the genital opening. The female portion has large oviduct glands, and a seminal receptacle, but no bursa copulatrix. During copulation one individual acts as a male and creeps on the dorsal surface of its partner's shell. The penis is everted and bent ventrally to reach the mantle cavity of the female partner, sperm being transferred in a spermatophore. Spermatophore structure and the position where they are deposited are species specific (Robertson 1978). Eggs are deposited in a mucous envelope or capsule. Each egg is separated from the other by secretions from the oviduct and attached by chalazae (see Robertson 1985b). Some species deposit spawn in crevices of stones and rocks where the adults live. Most species have a pelagic larval phase.

Pyramidellids are ectoparasites, feeding on the body fluids of various invertebrates, mainly polychaete worms and other molluscs (see Robertson & Orr 1961); many are not host specific (see Robertson & Mau-Lastovicka 1979 for review). They are

equipped with an elongate, acrembolic proboscis which, when not feeding, is normally withdrawn into a proboscis sheath. The entire anterior gut, including oral tube, buccal cavity and oesophagus, is elongate (Fig. 15.186H). The mouth region is converted into a sucker used to anchor the pyramidellid to its host. A stylet, in the form of a long, hollow, cylindrical, cuticular rod (a modified jaw), is used to pierce the skin of the host and is thrust out of the mouth of the stylet sheath by a complex series of muscles at its base. Body fluids are sucked from the host with the aid of a buccal pump and buccal bulb, situated at the base of the oral tube (Fretter & Graham 1949; Maas 1965; Wise 1993).

Pyramidellids will often stay on, or close to, their host. Species feeding on tubicolous polychaetes evert their proboscis and move it slowly and cautiously to the worm's tentacles. After touching the worm and initiating a jerk response, they find an appropriate spot on which to attach (Fretter & Graham 1949; Ponder 1973c). Merrill & Boss (1964) observed *Odostomia seminuda* feeding on the slipper limpet *Crepidula fornicata*. The parasite positioned itself on the edge of the host shell and inserted its proboscis beneath the shell into the mantle. This caused the host to clamp down its shell and the parasite hurriedly to withdraw its proboscis. Similar persistent, but intermittent feeding has been observed in pyramidellids feeding on gastropod species in genera such as *Crucibulum*, *Hydrobia*, and *Rissoa*, all of which retract into their shells when being consumed. Some bivalve hosts, such as *Ostrea edulis* and *Mytilus edulis*, react by depositing a barrier of shell material and withdrawing the affected portions; thus the parasite can eventually enter and live within the shell cavity of its host (Cole & Hancock 1955). However, no known pyramidellids have become highly modified internal parasites as have some Eulimidae.

Some commercially important species of molluscs are adversely affected by pyramidellids. Giant clams (*Tridacna* species) are attacked by various pyramidellids (Cumming 1988). Persistence of attack by pyramidellids on various oyster and mussel species can lead to loss of condition and, possibly, in severe cases, death (Cole & Hancock 1955). Ward & Langdon (1986) have shown that *Boonea impressa* affects the growth rate, filtration rate and valve movements of the North American rock oyster *Crassostrea virginica* and ultimately may affect the survival rate.

The majority of pyramidellids live in subtidal to deep water and prefer muddy or sandy bottoms (presumably because annelid worms are abundant in these habitats). Some species live intertidally.

The taxonomy of this large, diverse group is in a very poor state and is critically in need of revision. Only a few genera are listed below as examples. For each there are several closely related 'genera' which, because of space constraints, are not mentioned. *Turbonilla* is a worldwide genus that has very elongate shells with axial ribs and lacks a columellar plait. *Odostomia* (Fig. 15.186C) is a cosmopolitan genus which is well represented in Australia, and is characterised by small size, typically smooth shells with few whorls, a single columella fold and a conical to ovate spire. Species of *Chysallida* are similar in appearance to those of *Odostomia*, but have axial ribs. *Miralda* species have spiral cords and *Linopyrga* species have both (Fig. 15.186B). *Pyramidella* and allied genera, such as *Otopleura* (Fig. 15.186A) are large, live on sand flats in the tropics, and have up to three columellar plaits. Several genera are typified by their smooth, very elongate shells. Three which are especially noteworthy and are found in Australia are *Syrnola*, *Eulimella* and *Koloonella* (Fig. 15.186E). *Cingulina* species have very elongate shells with spiral cords. *Pseudoskenella* has a depressed, trochiform shell (Fig. 15.186F) and is common around south-eastern Australia living amongst the intertidal tube worm *Galeolaria* on which it feeds (Ponder 1973c).

Pyramidellids first appeared in the Cretaceous and are numerous in the Tertiary (Dall & Bartsch 1904; Wenz 1940a). They occur in the Tertiary of southern Australia and New Zealand (Laseron 1959).

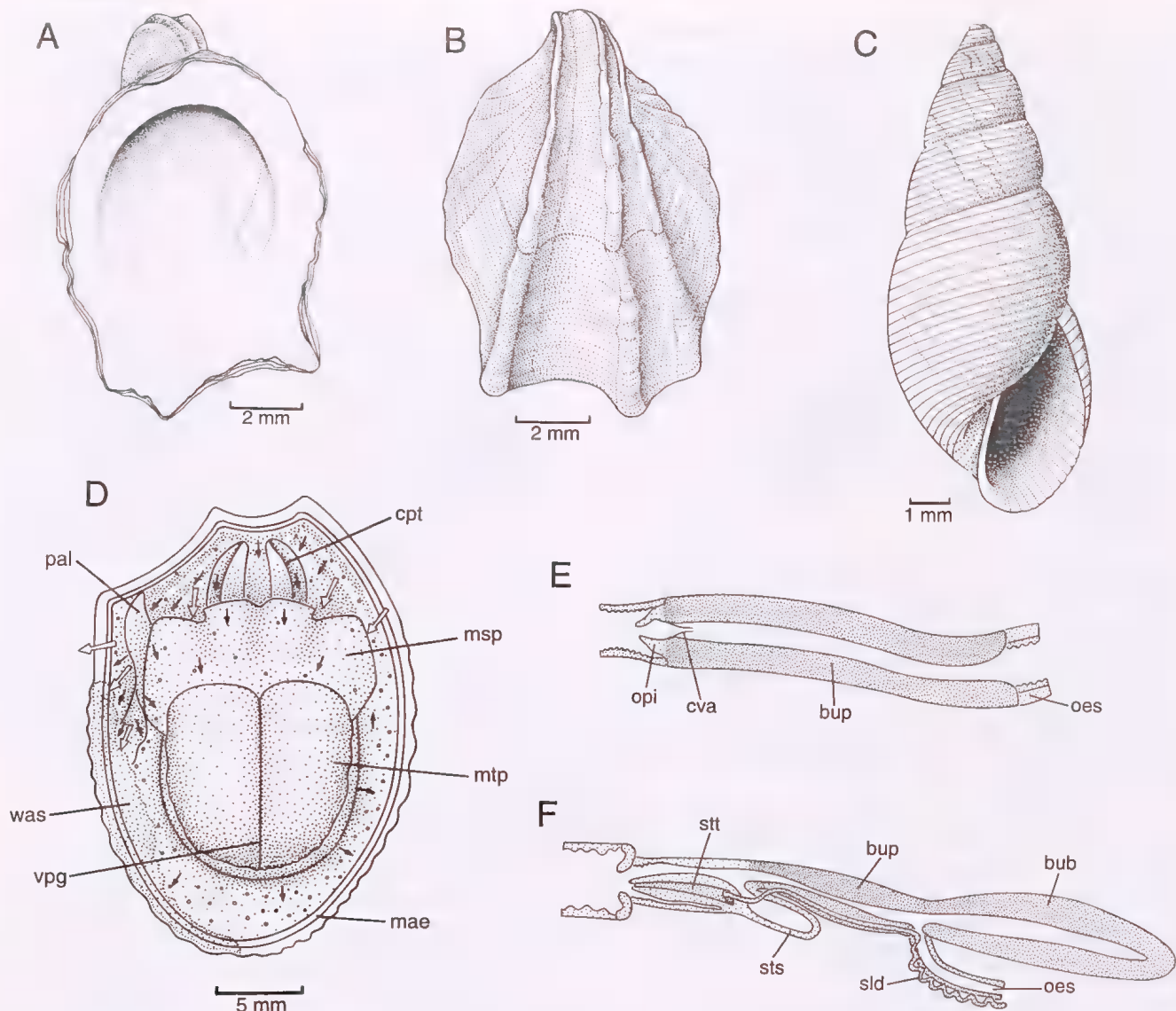


Figure 15.187 Family Amathinidae. A, B, *Amathina tricarinata*, shell: A, apertural view; B, dorsal view. C, *Leucotina concinna*, shell, apertural view; D, *Amathina tricarinata*, living animal, ventral view. E, F, diagrammatic transverse section of the buccal region showing the differences between *Amathina* sp. (E) and a pyramidellid (F). bub, buccal bulb; bup, buccal pump; cpt, cephalic tentacles; cva, chitinous 'valve'; mae, mantle edge; msp, mesopodium; mtp, metapodium; oes, oesophagus; opi, oral papilla; pal, pallial lobe; sld, salivary duct; sts, stylet sac; stt, stylet; vpg, ventral pedal groove; was, accumulated waste. (D–F, after Ponder 1988)

Family Amathinidae

Amathinids are small to medium-sized (20 mm) marine, limpet-like to coiled snails that live on large bivalves. They differ from pyramidellids in having the secondary gill situated to the left of the dorsal ciliated ridge in the pallial cavity, in lacking a hypobranchial gland, stylet and buccal bulb and in having diffuse salivary glands (Fig. 15.187E, F).

Until recently, the genus *Amathina* was included in either the Capulidae or the Hipponicidae, although Habe (1962) placed it in the Trichotropidae. Very little was known of the anatomy of *Amathina* until Ponder in 1987 showed it to be similar to that of pyramidellids and established a new family for this and several other genera.

The shells are either limpet-like or littoriniform to ovate-conic, the limpet-shaped shells have a horse-shoe-shaped shell muscle with the opening anterior as in 'prosobranch' limpets (Fig. 15.187A–C). The protoconch is only slightly heterostrophic and the periostracum is usually well developed. Sculpture is predominantly spiral with axial sculpture reduced to weak growth lamellae. An operculum may be absent or present.

The following description of anatomy is based on Ponder (1987). The foot has a thin, mobile mesopodium and a longitudinally divided, disc-like metapodium (Fig. 15.187D). The cephalic

tentacles are short, rabbit ear-shaped and have a deep cleft along the outer latero-ventral faces, in which cilia create a backwardly directed current. The mantle cavity has a pair of ciliated ridges on the right side of the plicate gill. There is a large, pigmented mantle gland to the right of the ciliated ridges. The kidney lies in the pallial roof and, like the nervous system, is very similar to that of pyramidellids. The nerve ring surrounds the proboscis sheath and the circumoesophageal ganglia are very concentrated.

Amathinids are simultaneous hermaphrodites, having an ovotestis which contains ripe sperm and ova. The penis is internal, simple, tapered and located in a sheath embedded in the pedal haemocoel. The female system is dominated by massive oviduct glands and in size and organisation resembles that of pyramidellids. The larvae of *Amathina tricarinata* are thought to be planktotrophic because of the small size of the eggs. Egg capsules are laid in clusters in jelly in *A. tricarinata*. Eggs are connected by chalazae and each egg is enclosed in a thin-walled capsule which is bound to others by small amounts of transparent jelly, and arranged in rows three or four capsules thick.

Feeding has not been observed. It is presumed, on the basis of anatomy and general lack of identifiable material in the gut, that amathinids are ectoparasitic. They live attached to large bivalves, close to the shell margin, usually in the vicinity of the exhalant siphon. They probably penetrate the body of the host

in a way similar to eulimids which also lack a radula, jaws or stylets (Smith 1984). The proboscis is very long, slender and complex in structure.

Amathina species have been found living on shells of various large bivalve species such as *Pinna* and *Pteria*, and ostreids (Habe 1961, 1962; Kay 1979; Morton, B. & Morton 1983; Ponder 1987). They leave a scar on the host's shell when removed and are somewhat mobile; as the host's shell grows they move to stay near the shell margin.

At present, only a few genera are recognised in this family but further studies will probably reveal others. *Amathina* is represented in Australia by *A. tricarinata*. *Amathina tricarinata* has a shell which is cap-shaped and bears three strong ridges that run from the apex to the anterior margin. *Leucotina* (Fig. 15.187C), an Indo-West Pacific genus, has been confirmed by Hori & Tsuchida (1995) to be amathinid. It has a pupiform shell.

The earliest known fossil amathinids are of the genus *Iselica* from the Eocene of North America (Wenz 1940b).

LITERATURE CITED

- Abbott, D.P. (1962). Observations on the gastropod *Terebellum terebellum* (Linnaeus), with particular reference to the behaviour of the eyes during burrowing. *The Veliger* 5: 1–3
- Abbott, R.T. (1949). Sexual dimorphism in Indo-Pacific *Strombus*. *The Nautilus* 63: 58–61
- Abbott, R.T. (1952). A study of an intermediate snail host (*Thiara granifera*) of the Oriental Lung Fluke (*Paragonimus*). *Proceedings of the United States National Museum* 102: 71–116
- Abbott, R.T. (1958). The gastropod genus *Assimineia* in the Philippines. *Proceedings of the Academy of Natural Sciences of Philadelphia* 110: 213–278
- Abbott, R.T. (1959). The family Vasidae in the Indo-Pacific. *Indo-Pacific Mollusca* 1: 15–32
- Abbott, R.T. (1960). The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca* 1: 33–144
- Abbott, R.T. (1961). The genus *Lambis* in the Indo-Pacific. *Indo-Pacific Mollusca* 1: 147–174
- Abbott, R.T. (1967). The genus *Terebellum* in the Indo-Pacific. *Indo-Pacific Mollusca* 1: 445–454
- Abbott, R.T. (1968). The helmet shells of the world (Cassidae). Part 1. *Indo-Pacific Mollusca* 2: 15–201
- Abbott, R.T. (1974). *American Seashells*. The marine Mollusca of the Atlantic and Pacific coasts of North America. Van Nostrand Reinhold Co. : New York 2nd edn 663 pp.
- Abdel-Hafez, S. & Ismail, N.S. (1983). Larval stages of digenetic trematodes of *Theodoxus jordani* (Sowerby, 1836) snails from Yarmouk River, Jordan. *Zeitschrift für Parasitenkunde* 69: 789–796
- Abrams, P. (1978). Shell selection and utilisation in a terrestrial hermit crab *Coenobita compressus*. *Oecologia (Heidelberg)* 34: 239–253
- Ackerly, S.C. (1989). Shell coiling in gastropods: analysis by stereographic projection. *Palaaios* 4: 374–378
- Afzelius, B.A. & Dallai, P. (1983). The paired spermatozoa of the marine snail, *Turritella communis* Lamarck (Mollusca, Mesogastropoda). *Journal of Ultrastructural Research* 85: 311–319
- Akpan, E.B., Farrow, G.E. & Morris, N. (1982). Limpet grazing on Cretaceous algal-bored ammonites. *Palaontology* 25: 361–367
- Alberch, P., Gould, S.J., Oster, G.F. & Wake, D.B. (1979). Size and shape in ontogeny and phylogeny. *Paleobiology* 5: 296–317
- Alexander, C.G. & Rae, J.C. (1974). The structure and formation of the crystalline style of *Telescopium telescopium* (Linnaeus) (Gastropoda: Prosobranchia). *The Veliger* 17: 56–60
- Allan, J. (1936). *Mysticoncha*, a new generic name for *Caledoniella* Basedow, non Souverbie. *Records of the Australian Museum* 19: 391–396
- Allan, J. (1950). *Australian Shells: with related animals living in the sea, in freshwater and on the land*. Georgian House : Melbourne xix 470 pp.
- Allan, J. (1956). *Cowry Shells of World Seas*. Georgian House : Melbourne x 170 pp.
- Allan, J. (1958). Some species of Lamellariidae (Class Gastropoda) from the eastern Australian coast. *Journal of the Malacological Society of Australia* 1(2): 48–57
- Allan, J. (1959). *Australian Shells: with related animals living in the sea, freshwater and on the land*. Georgian House : Melbourne 2nd edn xxi 487 pp.
- Allan, J. & Middleton, T.C. (1946). Observations on the egg case and young of the baler shell *Melo umbilicata* Brod. *Victorian Naturalist* 62: 172–177
- Allmon, W.D. (1988). Ecology of Recent turritelline gastropods (Prosobranchia: Turritellidae): current knowledge and paleontological implications. *Palaaios* 3: 259–284
- Allmon, W.D. (1990). Review of the *Bullia* group (Gastropoda: Nassariidae) with comments on its evolution, biogeography, phylogeny. *Bulletin of American Paleontology* 99: 1–759
- Allmon, W.D., Jones, D.S., Aiello, R.L., Gowlett-Holmes, K. & Probert, P.K. (1994). Observations on the biology of *Maoricolpus roseus* (Quoy & Gaimard) (Prosobranchia: Turritellidae) from New Zealand and Tasmania. *The Veliger* 37: 267–279
- Altes, J. (1978). Comparative use of shells by two sympatric *Clibanarius* spp. (Paguridae, Diogenidae). *Bulletin de la Société Zoologique de France* 103: 125–142
- Amaudrut, A. (1898). La partie antérieure du tube digestif et la torsion chez la Mollusques Gastéropodes. *Annales des Sciences Naturelles, Zoologie Série 7* 8: 1–291
- Ament, A.S. (1978). Geographic variation in relation to life history in three species of the marine gastropod genus *Crepidula*. *Dissertation Abstracts International B Sciences and Engineering* 39(3): 1123
- Amio, M. (1963). A comparative embryology of marine gastropods, with ecological considerations. *Journal of the Shimonoseki University of Fisheries* 12: 229–258
- Anderson, D.T. (1959). The reproduction and early life history of the gastropod *Cymatillesta spengleri* (Perry). *Proceedings of the Linnean Society of New South Wales* 84: 232–237
- Anderson, D.T. (1962). The reproduction and early life histories of the gastropods *Bembicium auratum* (Quoy and Gaimard) (Fam. Littorinidae), *Cellana tramoserica* (Sower.) (Fam. Patellidae) and *Melanerita melanotragus* (Smith) (Fam. Neritidae). *Proceedings of the Linnean Society of New South Wales* 87: 62–68
- Anderson, D.T. (1966). The reproduction and early life-histories of the gastropods *Notoacmea petterdi* (Ten. Woods), *Chiazacmaea flammea* (Quoy and Gaimard) and *Patelloida alticostata* (Angas) (Fam. Acmaeidae). *Proceedings of the Linnean Society of New South Wales* 90: 106–114
- Anderson, H. (1958). The gastropod genus *Bembicium* Phillippi. *Australian Journal of Marine and Freshwater Research* 9: 546–568
- Andrews, E.A. (1935). The egg capsules of certain Neritidae. *Journal of Morphology* 57: 31–59

15. PROSOBRANCHS

- Andrews, E.A. (1936). Spermatophores of the snail *Neritina reclivata*. *Journal of Morphology* 60: 191–209
- Andrews, E.B. (1964). The functional anatomy and histology of the reproductive system of some pilid gastropod molluscs. *Proceedings of the Malacological Society of London* 36: 121–140
- Andrews, E.B. (1965). The functional anatomy of the mantle cavity, kidney and blood system of some pilid gastropods (Prosobranchiata). *Journal of Zoology, London* 146: 70–94
- Andrews, E.B. (1976). The fine structure of the heart of some prosobranch and pulmonate gastropods in relation to filtration. *Journal of Molluscan Studies* 42: 199–216
- Andrews, E.B. (1979). Fine structure in relation to function in the excretory system of two species of *Viviparus*. *Journal of Molluscan Studies* 45: 186–206
- Andrews, E.B. (1981). Osmoregulation and excretion in prosobranch gastropods. Pt 2: structure in relation to function. *Journal of Molluscan Studies* 47: 248–289
- Andrews, E.B. (1985). Structure and function in the excretory system of archaeogastropods and their significance in the evolution of gastropods. *Philosophical Transactions of the Royal Society of London, Series B* 310: 383–407
- Andrews, E.B. (1988). Excretory systems of molluscs. Pp. 381–448 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca. Vol. 11. Form and Function*. Academic Press : San Diego
- Andrews, E.B. (1991). The fine structure and function of the salivary glands of *Nucella lapillus* (Gastropoda: Muricidae). *Journal of Molluscan Studies* 57: 111–126
- Andrews, E.B. (1992). The fine structure and function of the anal gland of the muricid *Nucella lapillus* (Neogastropoda) (and a comparison with that of the trochid *Gibbula cineraria*). *Journal of Molluscan Studies* 58: 297–313
- Andrews, E.B., Elphick, M.R. & Thorndyke, M.C. (1991). Pharmacologically active constituents of the accessory salivary and hypobranchial glands of *Nucella lapillus*. *Journal of Molluscan Studies* 57: 136–138
- Andrews, E.B. & Little, C. (1972). Structure and function in the excretory system of some terrestrial prosobranch snails (Cyclophoridae). *Journal of Zoology, London* 168: 395–422
- Andrews, E.B. & Little, C. (1982). Renal structure and function in relation to habitat in some cyclophorid land snails from Papua New Guinea. *Journal of Molluscan Studies* 48: 124–143
- Angas, G.F. (1871). A list of additional species of marine Mollusca to be included in the fauna of Port Jackson and the adjacent coasts of New South Wales. *Proceedings of the Zoological Society of London* 39: 87–101
- Angerer, G. & Haszprunar, G. (1996). Anatomy and affinities of lepid limpets (Patellogastropoda = Docoglossa). Pp. 171–175 in Taylor, J. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Ankel, W.E. (1926). Spermiogonienbildung durch atypische (apyrene) und typische Spermien bei *Scala* und *Janthina*. *Verhandlungen der Deutschen Zoologischen Gesellschaft 1925, Zoologischer Anzeiger, Supplement 2*: 193–202
- Ankel, W.E. (1929). Über die Bildung der Eikapsel bei *Nassa*-Arten. *Verhandlungen der Deutschen Zoologischen Gesellschaft 1928, Zoologischer Anzeiger, Supplement 4*: 219–230
- Ankel, W.E. (1930). Die atypische Spermatogenese von *Janthina* (Prosobranchia, Ptenoglossa). *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 11: 491–608
- Ankel, W.E. (1935). Das Gelege von *Lamellaria perspicua*. *Zeitschrift für Morphologie und Oekologie der Tiere* 30: 635–647
- Ankel, W.E. (1936a). Die Fressspuren von *Helcion* und *Littorina* und die Funktion der Radula. *Verhandlungen der Deutschen Zoologischen Gesellschaft, Zoologischer Anzeiger, Supplement 9*: 174–186
- Ankel, W.E. (1936b). Prosobranchia. Pp. 1–240 in Grimpe, G. & Wagler, E. (eds) *Tierwelt der Nord- und Ostsee* 29. Akademische Verlagsgesellschaft : Leipzig
- Ankel, W.E. (1937). Die feinere Bau der Kokons der Purpurschnecke *Nucella lapillus* (L.) und seine Bedeutung für das Laichleben. *Verhandlungen der Deutschen Zoologischen Gesellschaft 1936, Zoologischer Anzeiger, Supplement 10*: 77–86
- Ankel, W.E. (1938). Erwerb und Aufnahme der Nahrung bei den Gastropoden. *Verhandlungen der Deutschen Zoologischen Gesellschaft 1937, Zoologischer Anzeiger, Supplement 11*: 223–295
- Annandale, N. (1924). Note on the radula of *Pyrazus palustris*. *Records of the Indian Museum* 26: 549–551
- Annandale, N. & Prashad, B. (1921). The Indian molluscs of the estuarine subfamily Stenothyridae. *Records of the Indian Museum* 22(2)15: 121–136
- Ansell, A.D. & Morton, B. (1987). Alternative predation tactics of a tropical naticid gastropod. *Journal of Experimental Marine Biology and Ecology* 111: 109–119
- Antill, J. (1974). Another fossil ovoviviparous *Turritella*. *The Nautilus* 88: 67
- Appeldoorn, R.S. (1985). Growth, mortality and dispersion of juvenile, laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. *Bulletin of Marine Science* 37: 785–793
- Appeldoorn, R.S. (1988). Age determination, growth, mortality and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. *Fisheries Research (Amsterdam)* 6(4): 363–378
- Appleton, C.C. (1980). On the life-cycle of *Velacumantus australis* (Gastropoda: Potamididae) in the Swan Estuary, Western Australia. *Journal of the Malacological Society of Australia* 4: 252
- Arakawa, K.Y. (1963). Studies on molluscan faeces (I). *Publications of the Seto Marine Biological Laboratory* 11: 185–208
- Arakawa, K.Y. (1965). Studies on molluscan faeces (II). *Publications of the Seto Marine Biological Laboratory* 13: 1–21
- Arakawa, K.Y. (1968). Studies on molluscan faeces (III). *Publications of the Seto Marine Biological Laboratory* 16: 127–139
- Arakawa, K.Y. (1972). Studies on molluscan faeces (IV). *Publications of the Seto Marine Biological Laboratory* 19: 347–357
- Arakawa, K.Y. & Hayashi, S. (1972). On sexual dimorphism of fig shell, *Ficus subintermedia* (d'Orbigny). *Venus* 31: 63–71
- Aravindakshan, P.N. (1973). Distribution and ecology of *Pterotrachea coronata* (Forskål). Pp. 399–400 in Zeitschel, B. (ed.) *The Biology of the Indian Ocean. Vol. 3*. Springer-Verlag : Berlin
- Aravindakshan, P.N. (1977). Pterotracheidae (Heteropoda: Mollusca) of the Indian Ocean from the International Indian Ocean Expedition. Pp. 137–145 in *Proceedings of the Symposium on Warm Water Zooplankton*, Special Publication. National Institute of Oceanography : Goa
- Arnaud, P.M. & Van Mol, J.-J. (1979). Anatomy, ecology and distribution of the Volutidae and Volutomitridae of the southern Indian Ocean (Gastropoda: Prosobranchia). *The Veliger* 22: 19–31
- Arrontes, J. & Underwood, A.J. (1991). Experimental studies of some aspects of the feeding ecology of the intertidal starfish *Patriella exigua*. *Journal of Experimental Marine Biology and Ecology* 148: 255–269
- Asigau, W. (1988). *Strombus luhuanus* L. 1758 (Gastropoda: Mollusca) on the reefs near Gabagaba village, Papua New Guinea. *Science in New Guinea* 14: 40–46
- Azuma, M. (1965). On the radulae of the family Vexillidae. *Venus* 24: 53–57
- Bühlheim, H.-P. (1962). Elektronenmikroskopische Untersuchungen zur Feinstruktur der atypischen und typischen Spermatozoen von *Opalia crenimarginata* (Gastropoda, Prosobranchia). *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 56: 371–386
- Bühlheim, H.-P. (1968). Atypische Spermatozoenbildung bei *Epitonium tinctorum*. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 18: 232–253

- Bøggild, O.B. (1930). The shell structure of the Mollusks. *Det Kongelige Danske Videnskabernes Selskabs Skrifter. 9. Række, Naturvidenskabelig og Mathematisk Afdeling* 2: 231–326
- Bacci, G. (1947). L'inversione del sesso ed il ciclo stagionale della gonade in *Patella coerulea* L. *Pubblicazioni della Stazione Zoologica di Napoli* 21: 183–217
- Bacci, G. (1951). L'ermafroditismo di *Calyptrea chinensis* L. e di altri Calyptraeidae. *Pubblicazioni della Stazione Zoologica di Napoli* 23: 66–90
- Bahl, K.N. (1928). On the reproductive processes and development of *Pila globosa* (Swainson). I. Copulation and oviposition. *Memoirs of the Indian Museum* 9: 1–11
- Baker, H.B. (1922). Notes on the radulae of the Helicinidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 74: 29–67
- Baker, H.B. (1923). Notes on the radulae of Neritidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 75: 117–178
- Baker, H.B. (1925). Anatomy of *Hendersonia*: a primitive helicid mollusk. *Proceedings of the Academy of Natural Sciences of Philadelphia* 77: 273–303 [published 12 January 1926]
- Bandel, K. (1974a). Studies on Littorinidae from the Atlantic. *The Veliger* 17: 92–114
- Bandel, K. (1974b). Spawning and development of some Columbidae from the Caribbean Sea of Columbia (South America). *The Veliger* 18: 271–282
- Bandel, K. (1975). Entwicklung der Schale im Lebensablauf zweier Gastropoden Arten: *Buccinum undatum* und *Xancus angulatus* (Prosobranchier, Neogastropoda). *Biominalisation* 8: 67–91
- Bandel, K. (1976a). Observations on spawn, embryonic development and ecology of some Caribbean lower Mesogastropoda (Mollusca). *The Veliger* 18: 249–271
- Bandel, K. (1976b). Morphologie der Gelege und ökologische Beobachtungen an Buccinaceen (Gastropoda) aus der südlichen Karibischen See. *Bonner Zoologische Beiträge* 27: 98–133
- Bandel, K. (1982). Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken [Morphology and formation of the early ontogenetic shells of conchiferan mollusks]. *Facies* 7: 1–198
- Bandel, K. (1984). The radulae of Caribbean and other Mesogastropoda and Neogastropoda. *Zoologische Verhandlungen* 214: 1–188
- Bandel, K. (1986). The ammonitella: a model of formation with the aid of the embryonic shell of archaeogastropods. *Lethaia* 19: 171–180
- Bandel, K. (1988). Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden? *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 67: 1–33
- Bandel, K. (1990). Shell structure of the Gastropoda excluding Archaeogastropoda. Pp. 117–134 in Carter, J.G. (ed.) *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Vol. I.* Van Nostrand Reinhold: New York
- Bandel, K. (1991). Gastropoda from brackish and freshwater of the Jurassic–Cretaceous transition (a systematic reevaluation). *Berliner Geowissenschaftliche, Abhandlungen Reihe A Geologie und Paläontologie* 134: 9–55
- Bandel, K. (1993a). Caenogastropoda during Mesozoic times. *Scripta Geologica, Special Issue* 2: 7–56
- Bandel, K. (1993b). Character of a microgastropod fauna from a carbonate sand of Cebu (Philippines). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 71: 441–485
- Bandel, K. (1996). Some heterostrophic gastropods from Triassic St Cassian formation with a discussion on the classification of the Allogastropoda. *Paleontologicheskii Zhurnal* 70: 325–365
- Bandel, K. & El-Nakhal, H.A. (1993). The history and relationship of *Scaliola*, a gastropod that cements particles to its shell. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 75: 171–191
- Bandel, K. & Hemleben, C. (1987). Jurassic heteropods and their modern counterparts (planktonic Gastropoda, Mollusca). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 174: 1–22
- Bandel, K. & Kadolsky, D. (1982). Western Atlantic species of *Nodilittorina* (Gastropoda: Prosobranchia): comparative morphology and its functional, ecological, phylogenetic and taxonomic implications. *The Veliger* 25: 1–42
- Bandel, K. & Riedel, F. (1994). Classification of fossil and Recent Calyptraeidae (Caenogastropoda) with a discussion on neomesogastropod phylogeny. *Berliner Geowissenschaftliche, Abhandlungen E* 13: 329–367
- Bandel, K. & Wedler, E. (1987). Hydroid, amphineuran and gastropod zonation in the littoral of the Caribbean Sea, Colombia. *Senckenbergiana Maritima* 19: 1–129
- Barash, A. & Zenziper, Z. (1985). Structural and biological adaptations of Vermetidae (Gastropoda). *Bollettino Malacologico* 21: 145–176
- Barkati, S. & Ahmed, M. (1982). Studies on the reproductive biology of some prosobranchs from the coast of Karachi (Pakistan) bordering the northern Arabian Sea, 1: Observations on *Planaxis sulcatus* (Born, 1780). *The Veliger* 24: 355–358
- Basedow, H. (1905). On Naticoid genera *Lamellaria* and *Caledoniella* from South Australia. *Transactions of the Royal Society of South Australia* 29: 181–186
- Battershill, C.N. & Bergquist, P.R. (1982). Responses of an intertidal gastropod to field exposure of an oil and a dispersant. *Marine Pollution Bulletin* 13: 159–162
- Bayer, C. (1952). Catalogue of the genera *Melongena* and *Semifusus*. *Zoologische Mededelingen uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden* 31: 265–299
- Bayer, F.M. (1965). New pleurotomariid gastropods from the western Atlantic, with a summary of the Recent species. *Bulletin of Marine Science* 15: 737–796
- Bayliss, D.E. (1982). Switching by *Lepsiella vinosa* (Gastropoda) in South Australian mangroves. *Oecologia (Heidelberg)* 54: 212–226
- Bayliss, D.E. (1986). Selective feeding on bivalves by *Polinices alderi* (Forbes) (Gastropoda). *Ophelia* 25: 33–47
- Bayne, B.L. & Scullard, C. (1978). Rates of oxygen consumption by *Thais (Nucella) lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 32: 97–111
- Bayne, C.J. (1968). Histochemical studies on the egg capsules of eight gastropod molluscs. *Proceedings of the Malacological Society of London* 38: 199–212
- Bearup, A.J. (1955). A schistosome larva from the marine snail *Pyrazus australis* as a cause of cercarial dermatitis in man. *Medical Journal of Australia* (June 25) 1955: 955–960
- Bearup, A.J. (1956). The life cycle of *Austrotilharzia terrigalensis* Johnston 1917. *Parasitology* 46: 470–479
- Beck, L.A. (1992a). *Symmetromphalus hageni* sp. n. a new neomphalid gastropod (Prosobranchia: Neomphalidae) from hydrothermal vents at the Manus-Arc Basin (Bismarck Sea, Papua New Guinea). *Annalen Naturhistorischen Museums in Wien* 93: 243–257
- Beck, L.A. (1992b). Two new neritacean limpets (Gastropoda: Prosobranchia: Neritacea: Phenocolepidae) from active hydrothermal vents at Hydrothermal Field 1 'Wienerwald' in the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). *Annalen Naturhistorischen Museums in Wien* 93: 259–275
- Beck, L.A. (1993). Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). *Annalen Naturhistorischen Museums in Wien* 94/95: 167–179
- Beddome, C.E. (1897). Description of a new species of *Pupina* from Queensland. *Proceedings of the Linnean Society of New South Wales* 21: 814–815
- Behrens, D.W. (1980). The Lamelliariidae of the north eastern Pacific Ocean. *The Veliger* 22: 323–339
- Bennett, I. (1966). Some pelagic molluscs and associated animals in south-eastern Australian waters. *Journal of the Malacological Society of Australia* 1(9): 40–51
- Bentham Jutting, W.S.S. van (1948). Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. I. Critical revision of the Javanese operculate land-shells of the families Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae and Cochlostomatidae. *Treubia* 19: 539–604

15. PROSOBRANCHS

- Benthem Jutting, W.S.S. van (1956). Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. V. Critical revision of the Javanese freshwater gastropods. *Treubia* 23: 259–477
- Benthem Jutting, W.S.S. van (1959). Non-marine Mollusca of the North Moluccan islands Halmahera, Ternate, Batjan and Obi. *Treubia* 25: 25–87
- Benthem Jutting, W.S.S. van (1963). Non-marine Mollusca of west New Guinea. I. Mollusca from fresh and brackish waters. *Nova Guinea, Zoology* 20: 409–521
- Beovich, E.K. & Quinn, G.P. (1992). The grazing effect of limpets on the macroalgal community of a rocky intertidal shore. *Australian Journal of Ecology* 17: 75–82
- Berg, C.J. Jr (1974). A comparative ethological study of strombid gastropods. *Behaviour* 51: 274–322
- Berg, C.J. Jr (1975). Behavior and ecology of conch (Superfamily Strombacea) on a deep subtidal algal plain. *Bulletin of Marine Science* 25: 307–317
- Bergh, L.S.R. (1853). Bidrag til en Monografi af Marseniaderne, en Familie af de gastrøpode Mollusker. *Det Kongelige Danske Videnskabernes Selskabs Skrifter 5. Række, Naturvidenskabelig og matematisk Afdeling* 3: 239–359
- Bergh, L.S.R. (1886a). Die Marseniaden, eine vorläufige Mittheilung. *Zoologische Jahrbücher, Systematik* 1(1): 165–176
- Bergh, L.S.R. (1886b). Report on the Marseniadae collected by H.M.S. Challenger during the years 1873–1876. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873–76, Zoology* 15: 1–25
- Bergh, L.S.R. (1895). Beiträge zur Kenntnis der Strombiden, besonders der Gattung *Terebellum* Klein. *Zoologische Jahrbücher, Abtheilung Anatomie und Ontogenie* 8: 342–378
- Bergh, R. (1875). Malacologische Untersuchungen. In Semper, C. *Reisen im Archipel der Philippinen*. Heft 9, Pl. 41, fig. 10 Wiesbaden
- Bergh, R. (1890). Malacologische Untersuchungen, 3. Die Nudibranchien des 'Sunda-Meeress'. In Semper, C. *Reisen im Archipel der Philippinen* 17: 873–991
- Bergh, R. (1895). Beiträge zur Kenntnis der Coniden. *Nova Acta der Kaiserlich Leopoldinisch-Carolinische Deutschen Akademie der Naturforscher* 65: 67–214
- Bergh, R. (1896). Beitrag zur Kenntnis der gattungen *Narica* und *Onustus*. *Verhandlungen des Zoologisch-Botanischen Gesellschaft in Wien* 44: 200–212
- Berry, A.J. (1961). The habitats of some minute cyclophorids, hydrocenids and vertiginids on a Malayan limestone hill. *Bulletin of the National Museum, Singapore* 30: 101–105
- Berry, A.J. (1964a). Faunal zonation in mangrove swamps. *Bulletin of the National Museum, Singapore* 32: 90–98
- Berry, A.J. (1964b). The reproduction of the minute cyclophorid snail *Opisthostoma (Plecostoma) retrovertens* from a Malayan limestone hill. *Proceedings of the Zoological Society of London* 142: 655–663
- Berry, A.J. (1974). Reproductive condition in two Malayan freshwater viviparid gastropods. *Journal of Zoology, London* 174: 357–367
- Berry, A.J. & Kadri, A.B. Haji (1974). Reproduction in the Malayan freshwater cerithiaceous gastropod *Melanoides tuberculata*. *Journal of Zoology, London* 172: 369–381
- Berthold, T. (1991). Vergleichende Anatomie, Phylogenie und Historische Biogeographie der Ampullariidae (Mollusca, Gastropoda). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 29: 1–256
- Beu, A.G. (1969). The gastropod genus *Thalassocydon* Barnard, 1960. *New Zealand Journal of Marine and Freshwater Research* 3: 445–452
- Beu, A.G. (1976a). Arrival of *Semicassis pyrum* (Lamarck) and other tonnacean gastropods in the Southern Ocean during Pleistocene time. *Journal of the Royal Society of New Zealand* 6: 413–432
- Beu, A.G. (1976b). Revision of the Southwest Pacific species of *Morum* (Oniscidia) (Gastropoda: Cassidae). *Journal of the Malacological Society of Australia* 3: 223–231
- Beu, A.G. (1978). New records and species of Cymatiidae (Gastropoda: Prosobranchia) from the Kermadec Islands, Norfolk Ridge and New Zealand. *Journal of the Malacological Society of Australia* 4: 29–42
- Beu, A.G. (1981). Australian gastropods of the family Bursidae. Part 1. The families of Tonnacea, the genera of Bursidae, and revision of species previously assigned to *Tutufa* Jousseaume, 1881. *Records of the Australian Museum* 33: 248–324
- Beu, A.G. (1985). A classification and catalogue of living world Ranellidae (= Cymatiidae) and Bursidae. *Conchologists of America Bulletin* 13: 55–66
- Beu, A.G. (1987). Taxonomy of gastropods of the families Ranellidae (= Cymatiidae) and Bursidae. Pt 2. Descriptions of 14 new Indo-West Pacific species and subspecies, with revisions of related taxa. *New Zealand Journal of Zoology* 13: 273–355
- Beu, A.G. (1988). Taxonomy of gastropods of the families Ranellidae (= Cymatiidae) and Bursidae. Part 5. Early history of the families, with four new genera and recognition of the Family Personidae. Pp. 69–96 in Grant-Mackie, J.A., Masuda, K., Mori, K. & Ogasawara, K. (eds) *Professor Tamio Kotaka Commemorative Volume on Molluscan Paleontology*. Saito Ho-on Kai, Special Publication : Sendai No. 2
- Beu, A.G. (in press). Indo-West Pacific Ranellidae, Bursidae and Personidae. A monograph of the New Caledonian fauna, with revisions of related taxa. *Mémoires du Muséum National d'Histoire Naturelle*
- Beu, A.G. & Kay, A.E. (1988). Taxonomy of gastropods of the families Ranellidae (= Cymatiidae) and Bursidae. Pt IV. The *Cymatium pileare* complex. *Journal of the Royal Society of New Zealand* 18: 185–223
- Beu, A.G. & Maxwell, P.A. (1987). A revision of the fossil and living gastropods related to *Plesiotriton* Fischer, 1884 (Family Cancellariidae, Subfamily Plesiotritoninae, n. subfam.). With an appendix: Genera of Buccinidae Pisaninae related to *Colubraria* Schumacher, 1817. *New Zealand Geological Survey Paleontological Bulletin* 54: 1–140
- Beu, A.G. & Maxwell, P.A. (1990). Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 58: 1–518 [Illustrated by R.C. Brazier]
- Beu, A.G. & Ponder, W.F. (1979). A revision of the species of *Bolma* Risso, 1826 (Gastropoda: Turbinidae). *Records of the Australian Museum* 32: 1–68
- Bieler, R. (1986). Revision of genera and Indo-Pacific species in the family Architectonicidae. *American Malacological Bulletin* 4: 108–109
- Bieler, R. (1988). Phylogenetic relationships in the gastropod family Architectonicidae, with notes on the family Mathildidae (Allogastropoda). Pp. 205–240 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Bieler, R. (1990). Haszprunar's 'clado-evolutionary' classification of the Gastropoda – a critique. *Malacologia* 31: 371–380
- Bieler, R. (1992a). Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics* 23: 311–338
- Bieler, R. (1992b). *Tenagodus* or *Siliquaria*? Unravelling taxonomic confusion in marine 'worm-snails' (Cerithioidea: Siliquariidae). *The Nautilus* 106: 15–20
- Bieler, R. (1993). Architectonicidae of the Indo-Pacific (Mollusca: Gastropoda). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 30: 1–377
- Bieler, R. (1995). Mathildidae from New Caledonia and the Loyalty Islands (Mollusca: Gastropoda: Heterobranchia) - Résultats des Campagnes MUSORSTOM 14. *Mémoires du Muséum National d'Histoire Naturelle* 167: 595–641
- Bieler, R. & Hadfield, M.G. (1990). Reproductive biology of the sessile gastropod *Vermicularia spirata* (Cerithioidea: Turritellidae). *Journal of Molluscan Studies* 56: 205–219
- Bieler, R. & Mikkelsen, P.M. (1988). Anatomy and reproductive biology of two western Atlantic species of Vitrinellidae, with a case of protandrous hermaphroditism in the Rissoacea. *The Nautilus* 102: 1–29
- Bilgin, F.H. (1973). Studies on the functional anatomy of *Melanopsis praemorsa* (L.) and *Zemelanopsis trifasciata* (Gray). *Proceedings of the Malacological Society of London* 40: 379–393

- Binder, E. (1959). Anatomie et systématique des *Mélaniens* d'Afrique occidentale (Moll. Gastropoda). *Revue Suisse de Zoologie* 66: 735–759
- Bishop, L. (1979). Anatomical and electrophoretic differences between species of Australian Potamididae (Mollusca: Gastropoda). Unpublished MSc thesis, Macquarie University, North Ryde
- Bishop, M.J. (1980). Helicinid land snails with apertural barriers. *Journal of Molluscan Studies* 46: 241–246
- Bishop, M.J. (1981). The biogeography and evolution of Australian land snails. Pp. 923–954 in Keast, A. (ed.) *Ecological Biogeography of Australia*. [Monographiae Biologicae 41] Junk: The Hague
- Black, R. (1977). Population regulation in the intertidal limpet *Patelloida alticostata* (Angas, 1865). *Oecologia (Heidelberg)* 30: 9–22
- Black, R. (1979). Competition between intertidal limpets: an intrusive niche on a steep resource gradient. *Journal of Animal Ecology* 48: 401–412
- Black, R., Lymbery, A. & Hill, A. (1988). Form and function: Size of radular teeth and inorganic content of feces in a guild of grazing molluscs at Rottnest Island, Western Australia. *Journal of Experimental Marine Biology and Ecology* 121: 23–35
- Blackburn, M. (1956). Sonic scattering layers of heteropods. *Nature* 177: 374–375
- Blank, M.Ya. (1980). On the Late Cretaceous gastropod molluscs of the Koryak Plateau. Pp. 81–93 in Ablayev, A.G., Poyarkov, B.V. & Poyarkova, Z.N. (eds) *Fossil Molluscs of the Far East and Their Stratigraphic Significance*. Far Eastern Geological Institute, Academy of Sciences of the USSR: Vladivostok [In Russian]
- Boettger, C.R. (1954). Die Systematik der euthyneuren Schnecken. *Verhandlungen der Deutschen Zoologischen Gesellschaft, Tübingen, supplement* 18: 253–280
- Boghen, A. & Farley, J. (1974). Phasic activity in the digestive gland cells of the intertidal prosobranch *Littorina saxatilis* (Oliv.) and its relation to the tidal cycle. *Proceedings of the Malacological Society of London* 41: 41–56
- Bogi, C. (1984). *Cocculina labronica* n.sp.. *Bollettino Malacologico, Milano* 20: 155–160
- Bondesen, P. (1940). Preliminary investigations into the development of *Neritina fluviatilis* L. in brackish and fresh water. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 104: 283–318
- Born, I. von (1778). *Index Rerum Naturalium Musei Caesarei Vindobonensis Pars I^{ma} Testacea*. – Verzeichniss etc. Illust. Vindobonae xlii 458 pp.
- Boss, K.J. (1982). Mollusca. Pp. 945–1166 in Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. Vol. 1. McGraw-Hill Book Company: New York
- Boss, K.J. & Merrill, A.S. (1984). Radular configuration and the taxonomic hierarchy in the Architectonicidae (Gastropoda). *Occasional Papers on Mollusks*. Museum of Comparative Zoology, Harvard University 4(66): 349–411
- Bouchet, P. (1976). Mise en évidence d'une migration de larves véligères entre l'étage abyssal et la surface. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, Série D* 283: 821–824
- Bouchet, P. (1985). Les Triphoridae de Méditerranée et du proche Atlantique (Mollusca, Gastropoda). *Lavori della Società Malacologica Italiana* 21: 5–58
- Bouchet, P. (1989). A marginellid gastropod parasitizes sleeping fishes. *Bulletin of Marine Science* 45: 76–84
- Bouchet, P. (1990). Turrid genera and mode of development: the use and abuse of protoconch morphology. *Malacologia* 32: 69–77
- Bouchet, P. & Guillemot, H. (1978). The *Triphora perversa* – complex in Western Europe. *Journal of Molluscan Studies* 44: 344–356
- Bouchet, P. & Metivier, B. (1982). Living Pleurotomariidae (Mollusca: Gastropoda) from the South Pacific. *New Zealand Journal of Zoology* 9: 309–318
- Bouchet, P. & Warén, A. (1979). The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. *Sarsia* 64: 211–243
- Bouchet, P. & Warén, A. (1980). Revision of the north-east Atlantic bathyal and abyssal Turridae (Mollusca: Gastropoda). *Journal of Molluscan Studies, Supplement* 8: 1–119
- Bouchet, P. & Warén, A. (1985a). Revision of the northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca: Gastropoda). *Bollettino Malacologico, Supplemento* 1: 121–296
- Bouchet, P. & Warén, A. (1985b). Taxonomic notes on tropical deep water Buccinidae with descriptions of new taxa. *Résultats des Campagnes MUSORSTOM. Vol. 2. Mémoires du Muséum National d'Histoire Naturelle, Paris (A)* 133: 457–499
- Bouchet, P. & Warén, A. (1986). Revision of the northeast Atlantic bathyal and abyssal Aclididae, Eulimidae, Epitoniidae (Mollusca, Gastropoda). *Bollettino Malacologico Supplemento* 2: 299–576
- Bouchet, P. & Warén, A. (1993). Revision of the northeast Atlantic bathyal and abyssal Mesogastropoda. *Bollettino Malacologico, Supplemento* 3: 578–840
- Bourne, G.C. (1908). Contributions to the morphology of the group Neritacea of aspidobranch gastropods. Pt 1. The Neritidae. *Proceedings of the Zoological Society of London* 1908: 810–887
- Bourne, G.C. (1910). On the anatomy and systematic position of *Incisura (Scissurella) lytteltonensis*. *Quarterly Journal of Microscopical Science* 55: 1–47
- Bourne, G.C. (1911). Contributions to the morphology of the group Neritacea of the apsidobranch gastropods. Pt II. The Helicinidae. *Proceedings of the Zoological Society of London* 1911: 759–809
- Boutan, L. (1885). Recherches sur l'anatomie et le développement de la Fissurelle. *Archives de Zoologie Expérimentale et Générale. Deuxième Série*. 3: 1–173
- Bouvier, E.L. (1887). Système nerveux, morphologie générale et classification des Gastéropodes prosobranches. *Annales Sciences Naturelles (Zoology)* (7)3: 1–510
- Bouvier, E.L. (1888). Etude sur l'organisation des Ampullaires. *Mémoires de la Société Philomathique de Paris, centenaire volume* 1888: 63–85
- Boycott, A.E. (1919). Parthenogenesis in *Paludestrina jenkinsi*. *Journal of Conchology* 16: 1–54
- Brace, R. (1977a). The functional anatomy of the mantle complex and columellar muscle of tectibranch molluscs (Gastropoda, Opisthobranchia). *Philosophical Transactions of the Royal Society of London, Series B* 277: 1–56
- Brace, R. (1977b). Anatomical changes in nervous and vascular systems during the transition from prosobranch to opisthobranch organisation. *Transactions of the Zoological Society of London* 34: 1–25
- Branch, G.M. (1974a). The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 2. Reproductive cycles. *Transactions of the Royal Society of South Africa* 41: 111–160
- Branch, G.M. (1974b). The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. 3. Growth Rates. *Transactions of the Royal Society of South Africa* 41: 161–193
- Branch, G.M. (1975a). Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behaviour. *Journal of Animal Ecology* 44: 575–600
- Branch, G.M. (1975b). Notes on the ecology of *Patella concolor* and *Cellana capensis*, and the effects of human consumption on limpet populations. *Zoologica Africana* 10: 75–85
- Branch, G.M. (1976). Interspecific competition experienced by South African *Patella* species. *Journal of Animal Ecology* 45: 507–529
- Branch, G.M. (1981). The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology, Annual Review* 19: 235–380
- Branch, G.M. & Branch, M.L. (1980a). Competition between *Cellana tramoserica* (Sowerby) (Gastropoda) and *Patriella exigua* (Lamarck) (Asteroidea), and their influence on algal standing stocks. *Journal of Experimental Marine Biology and Ecology* 48: 35–49

15. PROSOBRANCHS

- Branch, G.M. & Branch, M.L. (1980b). Competition in *Bembicium auratum* (Gastropoda) and its effect on microalgal standing stock in mangrove mud. *Oecologia (Heidelberg)* 46: 106–114
- Branch, G.M. & Branch, M.L. (1981). Experimental analysis of intraspecific competition in an intertidal gastropod *Littorina unifasciata*. *Australian Journal of Marine and Freshwater Research* 32: 573–589
- Brandt, R.A.M. (1968). Description of new non-marine mollusks from Asia. *Archives für Molluskenkunde* 98: 213–289
- Brandt, R.A.M. (1974). The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde* 105: 423 pp. 30 pls
- Bratcher, T. & Cernohorsky, W.O. (1987). *Living Terebras of the World. A Monograph of the Recent Terebridae of the World*. American Malacologists : Melbourne, Florida 240 pp.
- Brawley, S.H. & Adey, W.H. (1982). *Coralliophila abbreviata*: a significant corallivore. *Bulletin of Marine Science* 32: 595–599
- Brazier, J. (1889). Mollusca. Lord Howe Island, zoology, geology and physical characters. *Australian Museum Memoir* 2: 22–30
- Broderip, W.P. (1827). In Knight, *Penny Encyclopedia*. London: 254
- Brown, A.C. (1982). The biology of sandy-beach whelks of the genus *Bullia* (Nassariidae). *Annual Review of Oceanography and Marine Biology* 20: 309–361
- Brown, A.C. & Trueman, E.R. (1982). Muscles that push snails out of their shells. *Journal of Molluscan Studies* 48: 97–98
- Brown, S.C. (1969). The structure and function of the digestive system of the mud snail *Nassarius obsoletus* (Say). *Malacologica* 9: 447–500
- Bruguère, J.G. (1789). [Buccinum] *Encyclopédie Méthodique ou par de matieres. Histoire Naturelle des Vers et Mollusques* 1: 236–285
- Buckland-Nicks, J. & Chia, F.-S. (1990). Egg capsule formation and hatching in the marine snail *Littorina sitkana*. *Philosophical Transactions of the Royal Society of London, Series B* 326: 159–176
- Buonaiuto, M.F. (1975). Notes on the genus *Pseudomalaxis* Fischer (Mollusca: Gastropoda) and its fossil species in Australia. *Transactions of the Royal Society of South Australia* 99: 21–29
- Burch, J.B. (1960). Chromosomes of *Pomatiopsis* and *Oncomelania*. *American Malacological Union Annual Report for 1959* 26: 15
- Burch, J.B. (1976). Outline of classification of Australian terrestrial Molluscs (native and introduced). *Journal of the Malacological Society of Australia* 3: 127–156
- Burger, J.W. & Thornton, C.S. (1935). A correlation between the food eggs of *Fasciolaria tulipa* and the apyrene spermatozoa of prosobranch molluscs. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 68: 253–257
- Burgess, C.M. (1970). *The Living Cowries*. A.S. Barnes : New Jersey xiv 389 pp.
- Burgess, C.M. (1985). *Cowries of the World*. Gordon Verhoef : Cape Town 289 pp.
- Burn, R. (1975). *Titiscania limacina* Bergh, 1875, an unusual gastropod new to Australia. *Australian Shell News* 11: 1
- Burn, R. (1976). Shell with a built-in nest. *Australian Shell News* 16: 3
- Bush, M.S. (1989). The ultrastructure and function of the oesophagus of *Patella vulgata* Linnaeus. *Journal of Molluscan Studies* 55: 111–124
- Cannon, L.R.G. (1975). On the reproductive biology of *Cerithium moniliferum* Kiener (Gastropoda, Cerithiidae) at Heron Island, Great Barrier Reef. *Pacific Science* 29: 353–359
- Cannon, L.R.G. (1979). Ecological observations on *Cerithium moniliferum* Kiener (Gastropoda: Cerithiidae) and its trematode parasites at Heron Island, Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 30: 365–374
- Carrick, N.A. (1980a). Aspects of the biology of *Gazameda gunni* (Reeve, 1849) a viviparous mesogastropod and potential 'indicator' of perturbation (sic) induced by sewage pollution. *Journal of the Malacological Society of Australia* 4: 254–255
- Carrick, N.A. (1980b). Aspects of the biology of molluscs on the continental shelf off Sydney, NSW with particular reference to the population biology of *Gazameda gunni* (Reeve, 1849). Unpublished MSc. thesis, University of Sydney, Sydney
- Carriker, M.R. (1943). On the structure and function of the proboscis in the common oyster drill *Urosalpinx cinerea* Say. *Journal of Morphology* 73: 441–506
- Carriker, M.R. (1955). Critical review of the biology and control of oyster drills *Urosalpinx* and *Eupleura*. *U.S. Fisheries and Wildlife Service, Special Scientific Reports on Fish* 148: 1–150
- Carriker, M.R. (1961). Comparative functional morphology of boring mechanisms in Gastropods. *American Zoologist* 1(2): 263–266
- Carriker, M.R. (1981). Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* 20: 403–422
- Carter, J.G. & Clark, G.R., III (1985). Classification and phylogenetic significance of molluscan shell microstructure. Pp. 50–72 in Broadhead, T.W. (ed.) *Mollusks, Notes for a Short Course*. University of Tennessee, Department of Geological Science, Studies in Geology Vol. 13
- Carter, J.G. & Hall, R.M. (1990). Part 3. Polyplacophora, Scaphopoda, Archeogastropoda and Paragastropoda (Mollusca). Pp. 29–51, pls 122–134 in Carter, J.G. (ed.) *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Vol. 2. Atlas and Index*. Van Nostrand Reinhold : New York
- Cate, C.N. (1973). A systematic revision of the Recent cypracid family Ovulidae. *The Veliger* 15 (Supplement): 1–116
- Cate, C.N. (1974). Five new species of Ovulidae from the Western Pacific. *The Veliger* 16: 381–384
- Cate, C.N. (1979). A review of the Triviidae. *Memoirs of the San Diego Society of Natural History* 10: 1–126
- Cather, J.N. (1973). Ovoviviparity in *Nassarius albus* (Gastropoda, Prosobranchia). *Journal de Conchyliologie* 110: 83–86
- Catterall, C.P. & Poiner, R. (1983). Age- and sex-dependent patterns of aggregation in the tropical gastropod *Strombus luhuanus*. *Marine Biology* 77: 171–182
- Cernohorsky, W.O. (1966). A study of mitrid radulae and a tentative generic arrangement of the family Mitridae (Mollusca: Gastropoda). *The Veliger* 9(2): 101–126
- Cernohorsky, W.O. (1968). Observations on *Hipponix conicus* (Schumacher, 1817). *The Veliger* 10: 275–280
- Cernohorsky, W.O. (1970). Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum* 8: 1–190
- Cernohorsky, W.O. (1971). The family Naticidae (Mollusca: Gastropoda) in the Fiji Islands. *Records of the Auckland Institute and Museum* 8: 169–208
- Cernohorsky, W.O. (1972). *Marine Shells of the Pacific. Vol. 2. Pacific Publications* : Sydney 411 pp.
- Cernohorsky, W.O. (1976). The taxonomy of some Indo-Pacific Mollusca. Part 4. With descriptions of new taxa and remarks on *Nassarius copperingi* (Smith). *Records of the Auckland Institute and Museum* 13: 111–129
- Cernohorsky, W.O. (1978). The taxonomy of some Indo-Pacific Mollusca. Part 6. *Records of the Auckland Institute Museum* 15: 67–86
- Cernohorsky, W.O. (1980). Revision of the Australian and New Zealand Tertiary and Recent temperate species of the family Costellariidae (Mollusca: Gastropoda). *Records of the Auckland Institute and Museum* 16: 109–169
- Cernohorsky, W.O. (1981). Revision of the Australian and New Zealand Tertiary and Recent species of the family Nassariidae (Mollusca: Gastropoda). *Records of the Auckland Institute Museum* 18: 137–192
- Cernohorsky, W.O. (1984). Systematics of the family Nassariidae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum* 14: 1–356
- Chaffe, C. & Lindberg, D.R. (1986). Larval biology of early Cambrian molluscs: the implications of small body size. *Bulletin of Marine Science* 39: 536–549

- Chaniotis, B.N., Butler, J.M.Jr, Ferguson, F.M. & Jobin, W.R. (1980a). Bionomics of *Tarebia granifera* (Gastropoda: Thiaridae) in Puerto Rico, an Asian vector of *Paragonimiasis westermani*. *Caribbean Journal of Science* 16: 81–90
- Chaniotis, B.N., Butler, J.M.Jr, Ferguson, F.M. & Jobin, W.R. (1980b). Thermal limits, desiccation tolerance, and humidity reactions of *Thiara (Tarebia) granifera muiensis* (Gastropoda: Thiaridae) host of the Asiatic lung fluke disease. *Caribbean Journal of Science* 16: 91–93
- Chaniotis, B.N., Butler, J.M.Jr, Ferguson, F.M. & Jobin, W.R. (1980c). Presence of males in Puerto Rican *Thiara (Tarebia) granifera* (Gastropoda: Thiaridae), a snail thought to be parthenogenetic. *Caribbean Journal of Science* 16: 95–97
- Chapin, D.M. & Roberts, P.A. (1980). Karyotypes of six eastern Pacific acmaeid gastropods. *The Veliger* 22: 225–231
- Chapman, F. (1912). New or little known Victorian fossils in the National Museum. Part 15. Some Tertiary Gastropoda. *Proceedings of the Royal Society of Victoria* 25: 186–192
- Chapman, F. & Gabriel, C.J. (1923). A revision and description of the Australian Tertiary Patellidae, Patelloididae, Cocculinidae, and Fissurellidae. *Proceedings of the Royal Society of Victoria* 36: 22–40
- Chapman, M.G. (1994a). Small-scale patterns of distribution and size-structure of the intertidal littorinid *Littorina unifasciata* (Gastropoda: Littorinidae) in New South Wales. *Australian Journal of Marine and Freshwater Research* 45: 635–652
- Chapman, M.G. (1994b). Small- and broad-scale patterns of distribution of the upper-shore littorinid *Nodilittorina pyramidalis* in New South Wales. *Australian Journal of Ecology* 19: 83–95
- Chapman, M.G. (1995a). Spatial patterns of shell shape of three species of co-existing littorinid snails in New South Wales, Australia. *Journal of Molluscan Studies* 61: 141–162
- Chapman, M.G. (1995b). Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia. *Marine Ecology Progress Series* 126: 191–202
- Chapple, E.H. (1941). New Species of Tertiary Mollusca from Victoria. *Memoirs of the National Museum of Victoria* 12: 119–124
- Chelazzi, G., Deneubourg, J.L. & Focardi, S. (1984). Cooperative interactions and environmental control in the intertidal clustering of *Neita textilis* (Gastropoda: Prosobranchia). *Behaviour* 90: 151–166
- Chelazzi, G. & Vannini, M. (1976). Researches on the coast of Somalia, the shore and the dune of Sar Uanle. Part 9. Coastward orientation after displacement in *Nerita textilis* (Gastropoda, Prosobranchia). *Monitore Zoologico Italiano Supplemento* 8: 161–178
- Chelazzi, G. & Vannini, M. (1980). Zonal orientation based on local visual clues in *Nerita plicata* L. (Mollusca, Gastropoda) at Aldabra Atoll. *Journal of Experimental Marine Biology and Ecology* 46: 147–156
- Chernogorenko, M.I., Komarova, T.I. & Kurandina, D.P. (1978). The life-cycle of the trematode *Plagioporus skrjabini* (Allocreadiata, Opecoelidae). *Parazitologiya* 12: 479–486
- Chilton, N.B. & Bull, C.M. (1984). Influence of predation by a crab on the distribution of the size-groups of three intertidal gastropods in South Australia. *Marine Biology* 83: 163–169
- Chilton, N.B. & Bull, C.M. (1986). Size-related selection of two intertidal gastropods by the reef crab *Ozius truncatus*. *Marine Biology* 93: 475–480
- Choquet, M. (1970). Etude cytologique de la gonade de *Patella vulgata* L. (Gastropoda: Prosobranchia) au cours du changement de sexe naturel. *Comptes Rendus des Séances de l'Académie des Sciences* 271D: 1387–1390
- Christiaens, J. (1973). Revision du genre *Patella* (Mollusca, Gastropoda). *Bulletin du Muséum National d'Histoire Naturelle, Zoologie* 121: 1305–1392
- Christiaens, J. (1975a). Revision provisoire des mollusques marins récents de la famille des Acmaeidae et description de deux nouveaux sous-genres: *Simplacmaea* nov. subgen. et *Collisellacmaea* nov. subgen. *Informations de la Société belge de Malacologie* 4: 3–18
- Christiaens, J. (1975b). Revision provisoire des mollusques marins récents de la famille des Acmaeidae (seconde partie). *Informations de la Société belge de Malacologie* 4: 91–116
- Christiaens, J. (1976). De familie Acmaeidae. *Gloria Maris* 5: 49–64
- Christiaens, J. (1979). Le genre *Pectinodonta* Dall, 1882 (Gastropoda, Acmaeidae). *Informations de la Société belge de Malacologie* 7: 17–22
- Chung, P.R. (1984). A comparative study of three species of Bithyniidae (Mollusca: Prosobranchia): *Parafossarulus manchouricus*, *Gabbia misella* and *Bithynia tentaculata*. *Malacological Review* 17: 1–66
- Cipriani, R. & Penchaszadeh, P.E. (1993). How does *Strombina* reproduce? Evidence from two Venezuelan species (Prosobranchia: Columbidae). *The Veliger* 36 (2): 178–184
- Clealand, D.M. (1954). A study of the habits of *Valvata piscinalis* (Müller) and the structure and function of the alimentary canal and reproductive system. *Proceedings of the Malacological Society of London* 30: 167–203
- Clench, W.J. (1947). The genera *Purpura* and *Thais* in the Western Atlantic. *Johnsonia* 2: 61–91
- Clench, W.J. (1949). Cyclophoridae and Pupinidae of Caroline, Fijian and Samoan Islands. *Bulletin of the Bernice P. Bishop Museum* No. 196: 1–52
- Clench, W.J. & Turner, R.D. (1948a). A catalogue of the family Truncatellidae with notes and descriptions of new species. *Occasional Papers on Mollusks* 1(13): 157–212
- Clench, W.J. & Turner, R.D. (1948b). The genus *Truncatella* in the Western Atlantic. *Johnsonia* 2(25): 149–164
- Clench, W.J. & Turner, R.D. (1952). The genera *Epitonium* (part II), *Depressiscala*, *Cylindriscala*, *Nystiella* and *Solutiscala* in the Western Atlantic. *Johnsonia* 2: 289–356
- Clench, W.J. & Turner, R.D. (1957). The family Cymatiidae in the Western Atlantic. *Johnsonia* 3: 189–244
- Clench, W.J. & Turner, R.D. (1960). The genus *Calliostoma* in the western Atlantic. *Johnsonia* 4: 1–80
- Clench, W.J. & Turner, R.D. (1964). The subfamilies Volutidae, Zidoninae, Odontocymbiolinae and Calliotectinae in the Western Atlantic. *Johnsonia* 4(43): 129–180
- Climo, F.M. (1973). The systematics, biology and zoogeography of the land snail fauna of Great Island, Three Kings Group, New Zealand. *Journal of the Royal Society of New Zealand* 3: 565–628
- Climo, F.M. (1974). Description and affinities of the subterranean molluscan fauna of New Zealand. *New Zealand Journal of Zoology* 1: 247–284
- Climo, F.M. (1975). The anatomy of *Gegania valkyrie* Powell (Mollusca, Heterogastropoda, Mathildidae) with notes on other heterogastropods. *Journal of the Royal Society of New Zealand* 5: 275–288
- Climo, F.M. (1977). Notes on the New Zealand hydrobiid fauna (Mollusca: Gastropoda: Hydrobiidae). *Journal of the Royal Society of New Zealand* 7: 67–77
- Coan, E. (1964). A proposed revision of the rissoacean families Rissoidae, Rissoinidae, Cingulopsidae (Mollusca: Gastropoda). *The Veliger* 6: 164–171
- Coan, E. (1965). A proposed reclassification of the family Marginellidae (Mollusca: Gastropoda). *The Veliger* 7(3): 184–194
- Coe, W.R. (1935). Sexual phases in prosobranch mollusks of the genus *Crepidula*. *Science* 81: 570–572
- Coe, W.R. (1936). Sexual phases in *Crepidula*. *Journal of Experimental Zoology* 72: 455–477
- Coe, W.R. (1938). Nutrition and sexuality in protrandric gastropods of the genus *Crepidula*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 74: 158–160
- Coe, W.R. (1942). The reproductive organs of the prosobranch mollusk *Crepidula onyx* and their transformation during the change from male to female phase. *Journal of Morphology* 70: 501–512
- Coe, W.R. (1944). Sexual differentiation in mollusks. II. Gastropods, amphineurans, scaphopods and cephalopods. *Quarterly Review of Biology* 19: 85–97

15. PROSOBRANCHS

- Cole, H.A. & Hancock, D.A. (1955). *Odostomia* as a pest of oysters and mussels. *Journal of the Marine Biological Association of the United Kingdom* 34: 25–31
- Conklin, E.G. (1897). The embryology of *Crepidula*. *Journal of Morphology* 13: 1–226
- Connolly, M. (1939). A monographic South African survey of non-marine South African Mollusca. *Annals of the South African Museum* 33: 1–660
- Cook, P.M. (1949). A ciliary feeding mechanism in *Viviparus viviparus* (L.). *Proceedings of the Malacological Society of London* 27: 265–271
- Cooling, M.P. & Boulton, A.J. (1993). Aspects of the hyporheic zone below the terminus of a South Australian arid-zone stream. *Australian Journal of Marine and Freshwater Research* 44: 411–426
- Coomans, H.E. & Clover, P.W. (1972). The genus *Rivomarginella* (Gastropoda, Marginellidae). *Beaufortia* 20: 69–75
- Covert, G.A. (1986). A review of marginellid egg capsules. *Marginella. Marginalia* 1(4): 13–19
- Covert, G.A. & Covert, H.K. (1995). Revision of the supraspecific classification of marginelliform gastropods. *The Nautilus* 109: 43–110
- Cossmann, A.E.M. (1901). *Essais de paléoconchologie comparée. Vol. 4.* Cossmann : Paris 293 pp. 10 pls
- Cossmann, M. (1894). Révision sommaire de la fauna du Terrain Oligocène marin aux environs d'Etampes. *Journal de Conchyliologie* 41: 297–363
- Cotton, B.C. (1932). Notes on Australian Mollusca, with descriptions of new genera and new species. *Records of the South Australian Museum* 4: 537–547
- Cotton, B.C. (1935a). Recent Australian Viviparidae and a fossil species. *Records of the South Australian Museum* 5: 339–344
- Cotton, B.C. (1935b). The Australian viviparous river snails. *Victorian Naturalist* 52: 96–99
- Cotton, B.C. (1944). Australian margin shells: Marginellidae. *South Australian Naturalist* 22(4): 9–17
- Cotton, B.C. (1949). Australian Recent and Tertiary Mollusca, family Marginellidae. *Records of the South Australian Museum* 9: 197–224
- Cotton, B.C. (1951). Australian Recent and Tertiary Mollusca, family Cerithiopsidae. *Records of the South Australian Museum* 9: 386–396
- Cotton, B.C. (1952). Australian Recent and Tertiary Mollusca. *Transactions of the Royal Society of South Australia* 75: 38–54
- Cotton, B.C. (1956). Family Scalidae. *Royal Society of South Australia, Malacological Section, Publication No. 9*, 4 pp.
- Cotton, B.C. (1957). *Australian Recent and Tertiary Species of the Molluscan Family Pyrenidae*. Privately published : Adelaide
- Cotton, B.C. (1959a). *South Australian Mollusca. Archaeogastropoda*. Handbook of the Flora and Fauna of South Australia. South Australian Government Printer : Adelaide 449 pp.
- Cotton, B.C. (1959b). Family Potamididae. *Royal Society of South Australia Malacological Section, pamphlet No. 13*: 1–4
- Cotton, B.C. (1960). Family Cerithiidae. *Royal Society of South Australia Malacological Section, pamphlet No. 2*: 1–4 [Revised]
- Cotton, B.C. & Godfrey, F.K. (1932). South Australian shells. Pt III. *South Australian Naturalist* 13: 35–86
- Cotton, B.C. & Woods, N.H. (1935). The correlation of Recent and fossil Turritellidae of southern Australia. *Records of the South Australian Museum* 5: 369–387
- Cowan, I.M. (1974). The west American Hipponicidae and the application of *Malluvium*, *Antisabia*, and *Hipponix* as generic names. *The Veliger* 16: 377–381
- Cox, J.C. (1868). *A Monograph of Australian Land Shells*. William Maddox : Sydney 110 pp.
- Cox, J.C. (1907). *A List of Cyclophoridae Found in Australia, New Guinea and Adjacent Groups of Islands*. F.W. White : Sydney 28 pp.
- Cox, L.R. (1960a). Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33: 239–261
- Cox, L.R. (1960b). Gastropoda. General characteristics of Gastropoda. Pp. 184–1169 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part I. Mollusca I.* Geological Society of America & University of Kansas Press : Boulder, Colorado & Lawrence, Kansas
- Creek, G.A. (1951). The reproductive system and embryology of the snail *Pomatias elegans* (Müller). *Proceedings of the Zoological Society of London* 121: 599–640
- Creese, R.G. (1980a). An analysis of distribution and abundance of populations of the highshore limpet *Notoacmea petterdi* (Tenison Woods). *Oecologia (Heidelberg)* 45: 252–260
- Creese, R.G. (1980b). Reproductive cycles and fecundities of four common eastern Australian archaeogastropod limpets (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 31: 49–59
- Creese, R.G. (1981). Patterns of growth, longevity and recruitment of intertidal limpets in New South Wales. *Journal of Experimental Marine Biology and Ecology* 51: 145–171
- Creese, R.G. (1982). Distribution and abundance of the acmaeid limpet *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia (Heidelberg)* 52: 85–96
- Creese, R.G. (1988). Ecology of molluscan grazers and their interactions with marine algae in north-eastern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* 22: 427–444
- Creese, R.G., Schiel, D.R. & Kingsford, M.J. (1990). Sex change in the giant limpet *Patella kermadecensis*, from the Kermadec Islands, Southwest Pacific Ocean. *Marine Biology* 104: 419–426
- Creese, R.G. & Underwood, A.J. (1982). Analysis of inter- and intra-specific competition amongst limpets with different methods of feeding. *Oecologia (Heidelberg)* 53: 337–346
- Cribb, T.H., Bray, R.A. & Barker, S.C. (1992). A review of the family Transversotrematidae (Trematoda: Digenea) with the description of a new genus, *Crusziella*. *Invertebrate Taxonomy* 6: 909–935
- Crisp, M. (1973). Fine structure of some prosobranch osphradia. *Marine Biology* 22: 231–240
- Crisp, M. (1981). Epithelial sensory structures of trochids. *Journal of the Marine Biological Association of the United Kingdom* 61: 95–106
- Crofts, D.R. (1929). *Haliotis*. *Liverpool Marine Biological Committee Memoirs* 29: 1–174
- Crofts, D.R. (1937). The development of *Haliotis tuberculata* with special reference to organogenesis and torsion. *Philosophical Transactions of the Royal Society, Series B* 228: 219–268
- Crofts, D.R. (1955). Muscle morphogenesis in primitive gastropods and its relation to torsion. *Proceedings of the Zoological Society of London* 125: 711–750
- Cuénot (1899). L'excretion chez les mollusques. *Archives de Biologie, Paris* 16: 49–96
- Cumming, R.L. (1988). Pyramidellid parasites in giant clam mariculture systems. Pp. 231–236 in Copland, J.W. & Lucas, J.S. *Great Clams in Asia and the Pacific*. Australian Centre for Aquiculture Research Monograph 9
- Cuvier, G. (1817–1829). *Le Regne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Deterville : Paris 2 vols*
- D'Asaro, C.N. (1965). Organogenesis, development, and metamorphosis in the Queen Conch, *Strombus gigas*, with notes on breeding habits. *Bulletin of Marine Science* 15: 359–416
- D'Asaro, C.N. (1969). The comparative embryogenesis and early organogenesis of *Bursa corrugata* Perry and *Distorsio clathrata* Lamarck (Gastropoda: Prosobranchia). *Malacologia* 9: 349–389
- D'Asaro, C.N. (1970a). Egg capsules of prosobranch mollusks from south Florida and the Bahamas and notes on spawning in the laboratory. *Bulletin of Marine Science* 20: 414–440
- D'Asaro, C.N. (1970b). Egg capsules of some prosobranchs from the Pacific coast of Panama. *The Veliger* 13: 37–43

- D'Asaro, C.N. (1988). Micromorphology of neogastropod egg capsules. *The Nautilus* 102: 134–148
- D'Asaro, C.N. (1991). Gunnar Thorson's world-wide collection of prosobranch egg capsules: Muricidae. *Ophelia* 35: 1–101
- D'Asaro, C.N. (1993). Gunnar Thorson's world-wide collection of prosobranch egg capsules: Nassariidae. *Ophelia* 38: 149–215
- da Silva, F.M. & Brown, A.C. (1985). Egg capsules and veligers of the whelk *Bullia digitalis* (Gastropoda: Nassariidae). *The Veliger* 28: 200–203
- Daguzan, J. (1971). Contribution à l'étude de l'excrétion azotée chez *Littorina littorea* (L.) adulte (Mollusque Mésogastropode Littorinidae). *Archives des Sciences Physiologiques* 25: 293–302
- Dakin, W.J. (1912). Memoirs. No. 20. *Buccinum*. (The Welk). *Proceedings and Transactions of the Biological Society, Liverpool* 26: 253–367
- Dakin, W.J. (1952). *Australian Seashores. A guide for the beach-lover, the naturalist, the shore fisherman, and the student*. Angus & Robertson: Sydney xii 372 pp.
- Dales, R.P. (1953). The distribution of some heteropod molluscs off the Pacific coast of North America. *Proceedings of the Zoological Society of London* 122: 1007–1015
- Dall, W.H. (1871a). On the limpets; with special reference to the species of the west coast of America, and to a more natural classification of the group. *American Journal of Conchology* 6: 227–282
- Dall, W.H. (1871b). Preliminary sketch of a natural arrangement of the order Docoglossa. *Proceedings of the Boston Society of Natural History* 14: 49–55
- Dall, W.H. (1882). On certain limpets and chitons from the deep waters off the eastern coast of the United States. *Proceedings of the United States National Museum* 81: 400–426
- Dall, W.H. (1889). Reports on the results of dredging ... Report on the Mollusca. Part 2: Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoology* 18: 1–492, pls 10–40
- Dall, W.H. (1908). Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross" ... XIV. The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology* 43: 205–487, pls 1–22
- Dall, W.H. & Bartsch, P. (1904). Synopsis of the genera, subgenera and sections of the family Pyramidellidae. *Proceedings of the Biology Society of Washington* 17: 1–16
- Dan, J.C. & Wada, S.K. (1955). Studies on the acrosome. IV. The acrosome reaction in some bivalve spermatozoa. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 109: 40–55
- Dantart, L. & Luque, A. (1994). Cocculiniformia and Lepetidae (Gastropoda: Archaeogastropoda) from the Iberian waters. *Journal of Molluscan Studies* 60: 277–313
- Darling, S. (1965). Observations on the growth of *Cypraea spadicea*. *The Veliger* 8: 14–15
- Darragh, T.A. (1969). A revision of the family Columbariidae (Mollusca: Gastropoda). *Proceedings of the Royal Society of Victoria* 83: 63–119
- Darragh, T.A. (1970). Catalogue of Australian Tertiary Mollusca (except chitons). *Memoirs of the National Museum of Victoria* 31: 125–212
- Darragh, T.A. (1971). Revision of the Australian Tertiary Volutidae (Mollusca: Gastropoda). I. The subfamily Athletinae. *Journal of the Malacological Society of Australia* 2(2): 163–185
- Darragh, T.A. (1985). Molluscan biogeography and biostratigraphy of the Tertiary of southeastern Australia. *Alcheringa* 9: 83–116
- Darragh, T.A. (1987). Columbariinae (Gastropoda: Turbinellidae) from Queensland, Australia. *Proceedings of the Royal Society of Victoria* 99: 127–134
- Darragh, T.A. (1989). A revision of the Tertiary Volutidae (Mollusca: Gastropoda) of southeast Australia. *Memoirs of the Museum of Victoria* 49: 195–307
- Darragh, T.A. (1991). A revision of the Australian genus *Tylospira* Harris, 1897 (Gastropoda: Struthiolariidae). *Alcheringa* 15: 151–175
- Darragh, T.A. & Kendrick, G.W. (1994). Maastrichtian Scaphopoda and Gastropoda from the Miria Formation, Carnarvon Basin, northwestern Australia. *Records of the Western Australian Museum, Supplement No. 48*: 1–76
- Dautzenberg, P. & Fischer, H. (1900). Description d'un mollusque nouveau (*Bathysciadium conicum*). *Bulletin de la Société Zoologique de France* 24: 207–209
- Davies, P.S. (1969). Physiological ecology of *Patella*. III. Desiccation effects. *Journal of the Marine Biological Association of the United Kingdom* 49: 291–304
- Davis, G.M. (1967). The systematic relationship of *Pomatiopsis lapidaria* and *Oncomelania hupensis formosana* (Prosobranchia: Hydrobiidae). *Malacologia* 6: 1–143
- Davis, G.M. (1969). A taxonomic study of some species of *Semisulcospira* in Japan (Mesogastropoda: Pleuroceridae). *Malacologia* 7: 211–294
- Davis, G.M. (1971). Systematic studies of *Brotia costula episcopalis*, first intermediate host of *Paragonimus westermani* in Malaysia. *Proceedings of the Academy of Natural Sciences, Philadelphia* 123: 53–86
- Davis, G.M. (1972). Geographic variation in *Semisulcospira libertina* (Mesogastropoda: Pleuroceridae). *Proceedings of the Malacological Society of London* 40: 5–32
- Davis, G.M. (1979). The origin and evolution of the gastropod family Pomatiopsidae with emphasis on the Mekong River Triculinae. *Academy of Natural Sciences of Philadelphia, Monograph* 20: 1–120
- Davis, G.M. (1980). Snail hosts of Asian *Schistosoma* infecting man: evolution and coevolution. Pp. 195–238 in Bruce, J.I. & Sormmani, S. (eds) *The Mekong Schistosome*. Malacological Review Supplement 2
- Davis, G.M. (1981). Different modes of evolution and adaptive radiation in the Pomatiopsidae (Prosobranchia: Mesogastropoda). *Malacologia* 21: 209–262
- Davis, G.M., Chen, C.-E., Xing, X.-G. & Wu, C. (1988). The Stenothyridae of China. No. 2. *Stenothyra hunanensis*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 140: 247–266
- Davis, G.M. & Pons da Silva, M.C. (1984). *Potamolithus*: morphology, convergence, and relationships among hydrobioid snails. *Malacologia* 25: 73–108
- Davis, G.M., Yuan Hua Guo, Hoagland, K.E., Ling Cai Zheng, Hong Mu Yang & Yuang Fan Zhou (1986a). Anatomy of *Stenothyra divalis* from the People's Republic of China and description of a new species of *Stenothyra* (Prosobranchia: Rissoacea: Stenothyridae). *Proceedings of the Academy of Natural Sciences of Philadelphia* 138: 318–349
- Davis, G.M., Yuan Hua Guo, Hoagland, K.E., Pu Lin Chen, Ling Cai Zheng, Hong Mu Yang, De Ji Chen & Yuang Fan Zhou (1986b). Anatomy and systematics of *Triculini* (Prosobranchia: Pomatiopsidae: Triculinae), freshwater snails from Yunnan, China, with descriptions of new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 138: 466–575
- Day, J.A. (1969). Feeding of the cymatiid gastropod, *Argobuccinum argus*, in relation to the structure of the proboscis and secretions of the proboscis gland. *American Zoologist* 9: 909–916
- Dazo, B.C. (1965). The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). *Malacologia* 3: 1–80
- de Blainville, M.H. (1825–1827). *Manuel de Malacologie et de Conchologie etc.* Levraut: Paris viii 664 pp.
- de Follin, L. (1875). *Monographie de la Famille des Caecidae*. A. Laignere: Bayonne 31 pp.
- Delhay, W. (1974). Contribution à l'étude des glandes pédieuses de *Pomatias elegans* (Mollusque, Gastéropode, Prosobranchie). *Annales des Sciences Naturelles, Zoologie* (12) 16: 97–110
- Delhay, W. (1976). Histophysiologie comparée des organes rénaux chez les Archaeogastéropodes (Mollusca-Prosobranchia). *Cahiers de Biologie Marine* 17: 305–322
- Delpey, G. (1941). Histoire du Genre *Campanile*. *Annales de Paléontologie* 24: 3–25

- Demian, E.S. & Yousif, F. (1973). Embryonic development and organogenesis in the snail *Marisa cornuarietis* (Mesogastropoda: Ampullariidae). 3. Development of the circulatory and renal systems. *Malacologia* 12: 175–194
- Dennant, J. & Kitson, A.E. (1903). Catalogue of the described species of fossils (except Bryozoa and Foraminifera) in the Cainozoic fauna of Victoria, South Australia and Tasmania. *Records of the Geological Survey of Victoria* 1: 89–147
- Denny, M.W. (1984). Mechanical properties of pedal mucus and their consequences for gastropod structure and performance. *American Zoologist* 24: 23–36
- Deshpande, R.D. (1957). Observations on the anatomy and biology of British trochids. PhD thesis, University of Reading, Reading
- Dick, R.S. (1964). Frequency patterns of arid, semi-arid and humid climate in Queensland. *Capricornia* 1: 21–30
- Diehl, M. (1956). Die Raubschnecke *Velutina velutina* als Feind und Bruteinmieter der Ascidie *Styela coriacea*. *Kieler Meeresforschungen* 12: 180–185
- Dockery, D.T. (1993). The streptoneuran gastropods, exclusive of the Stenoglossa, of the Coffee Sand (Campanian) of northeastern Mississippi. *Mississippi Department of Environmental Quality, Office of Geology, Bulletin* 129: 1–191
- Dodd, J.M. (1957). Artificial fertilisation, larval development and metamorphosis in *Patella vulgata* L. and *Patella coerulea* L. *Pubblicazioni della Stazione Zoologica di Napoli* 29: 172–186
- Dohmen, M.E. (1983). The polar lobe in eggs of molluscs and annelids: structure, composition and function. *Marine Biological Laboratory, Lectures in Biology* 2: 197–220
- Driscoll, A.N. (1972). Structure and function of the alimentary tract of *Batillaria zonalis* and *Cerithidea californica*, style-bearing mesogastropods. *The Veliger* 14: 375–386
- Drummond, I.M. (1902). Note on the development of *Paludina vivipara*, with special reference to the urinogenital organs and theories of gastropod torsion. *Quarterly Journal of Microscopical Science* 46: 97–143
- Dudgeon, D. (1982). The life history of *Brotia hainanensis* (Brot, 1872) (Gastropoda: Prosobranchia: Thiariidae) in a tropical forest stream. *Zoological Journal of the Linnean Society* 76: 141–154
- Dudgeon, D. (1986). The life cycle, population dynamics and productivity of *Melanoides tuberculata* (Muller, 1774) (Gastropoda: Prosobranchia: Thiariidae) in Hong Kong. *Journal of Zoology, London* 208: 37–53
- Dudgeon, D. (1989). Ecological strategies of Hong Kong Thiariidae (Gastropoda: Prosobranchia). *Malacological Review* 22: 39–53
- Duerr, F.G. (1968). Excretion of ammonia and urea in seven species of marine prosobranch snails. *Comparative Biochemistry and Physiology* 26: 1051–1059
- Dundee, D.S. (1957). Aspects of the biology of *Pomatiopsis lapidaria* (Say) (Mollusca: Gastropoda: Prosobranchia). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* 100: 1–65
- Dundee, D.S. & Cancienne, A.E. (1978). Louisiana citrus being damaged by snails. *The Nautilus* 92: 55–56
- Dzik, J. (1982). Larval development and relationships of *Mimospira* – a presumably hyperstrophic Ordovician gastropod. *Geologiska Föreningens i Stockholm Förhandlingar* 104: 231–239 [1983]
- Eernisse, D.J. & Reynolds, P.D. (1994). Polyplacophora. Pp. 55–110 in Harrison, F.W. & Kohn, A.J. (eds) *Microscopic Anatomy of Invertebrates. Vol. 5 Mollusca I*. Wiley-Liss: New York
- Eisenberg, J.M. (1981). *A Collector's Guide to Seashells of the World*. MacGraw-Hill Book Co.: New York 239 pp.
- Emerson, W.K. (1981). Two new Indo-Pacific species of *Morum* (Gastropoda: Tonnacea). *The Nautilus* 95: 101–105
- Emerson, W.K. (1985). Remarks on some Western Pacific species of *Morum* (Gastropoda: Tonnacea). *Stratigraphy, Palaeontology, Malacology. Special Publication No. 5*. Department of Mines & Energy, South Australia: 51–56
- Emerson, W.K. & Cernohorsky, W.O. (1973). The genus *Drupa* in the Indo-Pacific. *Indo-Pacific Mollusca* 3(13): 1–40
- Erwin, D.H. & Signor, P.W. (1991). Extinction in an extinction-resistant clade: the evolutionary history of the Gastropoda. Pp. 152–160 in Dudley, E.C. (ed.) *The Unity of Evolutionary Biology. Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, University of Maryland, July 1990 I*. Dioscordides Press: Portland, Oregon
- Eschsholtz, F. (1833). Genus *Acmaea*. Pp. 1–28 in Rathke, H. (ed.) *Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Thierarten, während des Flottcapitains von Kotzebue Zweiter Reise um die Welt ... in ... 1823–26 beobachten von ... F. Eschscholtz*. 1(5)
- Ewers, W.H. (1963). Some observations on the life cycle of *Velacumantus australis* (Quoy & Gaimard) (Gastropoda: Potamididae). *Journal of the Malacological Society of Australia* 7: 62–71
- Ewers, W.H. (1966). Polymorphism in fossil *Velacumantus australis* (Gastropoda: Potamididae). *Australian Journal of Zoology* 14: 867–875
- Ewers, W.H. (1967a). The distribution of *Velacumantus australis* (Gastropoda: Potamididae). *Australian Journal of Zoology* 15: 581–591
- Ewers, W.H. (1967b). Selection pressures and polymorphism in *Velacumantus australis* (Quoy and Gaimard). *Australian Journal of Zoology* 15: 727–728
- Ewers, W.H. (1967c). Geographic variation in the snail *Velacumantus australis* (Gastropoda: Potamididae). *Australian Journal of Zoology* 15: 1163–1171
- Ewers, W.H. & Rose, C.R. (1965). Trematode parasitism and polymorphism in a marine snail. *Science* 148: 1747–1748
- Ewers, W.H. & Rose, C.R. (1966a). The separation and identification of small juveniles of the species *Velacumantus australis* and *Pyrazus ebeninus* (Gastropoda, Potamididae). *Journal of the Malacological Society of Australia* 1(9): 36–39
- Ewers, W.H. & Rose, C.R. (1966b). Polymorphism in *Velacumantus australis* (Gastropoda, Potamididae) and its relationship to parasitism. *Australian Journal of Zoology* 14: 49–64
- Fair, R.H. (1976). *The Murex Book: an illustrated catalogue of recent Muricidae* (Muricinae, Muricopsinae, Ocenebrinae). R.H. Fair: Honolulu ix-xvi 138 pp.
- Fairweather, P.G. (1988). Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology Progress Series* 45: 237–243
- Fenchel, T. (1975). Factors determining distribution patterns of mud snails (Hydrobiidae). *Oecologia (Heidelberg)* 20: 1–17
- Field, L.H. (1977). An experimental analysis of the escape response of the gastropod *Strombus maculatus*. *Pacific Science* 31: 1–11
- Finlay, H.J. (1927a). A further commentary on New Zealand molluscan systematics. *Transactions and Proceedings of the New Zealand Institute* 57: 320–485
- Finlay, H.J. (1927b). New specific names for Austral Mollusca. *Transactions and Proceedings of the New Zealand Institute* 57: 488–533
- Finlay, H.J. & Marwick, J. (1937). The Wangaloan and associated molluscan faunas of Kaitangata–Green Island, Subdivision. *New Zealand Geological Survey Paleontological Bulletin* 15: 1–140
- Fioroni, P. (1982). Larval organs, larvae, metamorphosis and types of development of Mollusca – a comprehensive review. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 108: 375–420
- Fioroni, P., Oehlmann, J. & Stroben, E. (1991). The pseudohermaphroditism of prosobranchs; morphological aspects. *Zoologischer Anzeiger* 226: 1–26
- Fischer, P. (1862). Sur l'anatomie des *Hipponyx*. *Journal de Conchyliologie* 10: 1–17
- Fischer, P. (1880–1887). *Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles, suivi d'un appendice sur les Brachiopodes par D.P. Ehlert*. Librairie F. Savy: Paris xxiv 1369 pp.

- Fischer, P.-H. (1931). Recherches sur la vie ralentie de l'escargot (*Helix pomatia*). *Journal de Conchyliologie* 75: 5–100, 112–200
- Fischer, P.-H. (1948). Données sur la résistance et le vitalité des mollusques. *Journal de Conchyliologie* 88: 100–140
- Flecker, H. (1936). Cone shell mollusc poisoning, with report of a fatal case. *Medical Journal of Australia* 1936 (1): 464–466
- Fleming, J. (1828). *A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of Quadrupeds, Birds, Reptiles, Fishes, Molluscs, and Radiata of the United Kingdom, etc.* Bell & Bradfute: Edinburgh xxiii 565 pp.
- Fleming, C.A. (1963). The nomenclature of biogeographic elements in the New Zealand biota. *Transactions of the Royal Society of New Zealand* 1: 13–22
- Fletcher, W.J. (1984a). Variability in the reproductive effort of the limpet, *Cellana tramoserica*. *Oecologia (Heidelberg)* 61: 259–264
- Fletcher, W.J. (1984b). Intraspecific variation in the population dynamics and growth of the limpet, *Cellana tramoserica*. *Oecologia (Heidelberg)* 63: 110–121
- Fletcher, W.J. (1987). Life history dynamics of the limpet *Patelloida alticostata* in intertidal and subtidal environments. *Marine Ecology Progress Series* 39: 115–127
- Fletcher, W.J. (1988a). Reproductive effort in two subtidal populations of the limpet, *Patelloida mufria*. *Oecologia (Heidelberg)* 74: 586–591
- Fletcher, W.J. (1988b). Intraspecific interaction between adults and juveniles of the subtidal limpet, *Patelloida mufria*. *Oecologia (Heidelberg)* 75: 272–277
- Fletcher, W.J. & Creese R.G. (1985). Competitive interactions between co-occurring herbivorous gastropods. *Marine Biology* 86: 183–191
- Fletcher, W.J. & Underwood, A.J. (1987). Interspecific competition among subtidal limpets: effect of substratum heterogeneity. *Ecology* 68: 387–400
- Fleure, H.J. (1902). Notes on the relations of the kidney in *Haliotis tuberculata*, etc. *Quarterly Journal of Microscopical Science* 46: 77–96
- Fleure, H.J. (1904). On the evolution of topographical relationships among the Docoglossa. *Transactions of the Linnean Society of London, second series* 9: 269–290
- Fleure, H.J. (1905). Zur anatomie und Phylogenie von *Haliotis*. *Jenaische Zeitschrift für Naturwissenschaft* 39: 245–322
- Foin, T.C. (1976). Plate tectonics and the biogeography of the Cypraeidae (Mollusca: Gastropoda). *Journal of Biogeography* 3: 19–34
- Forbes, V.E. & Lopez, G.R. (1989). The role of sediment particle size in the nutritional energetics of a surface deposit-feeder. I. Ingestion and absorption of sedimentary microalgae by *Hydrobia truncata* (Vanatta). *Journal of Experimental Marine Biology and Ecology* 126: 181–192
- Ford, J.I. (1979). Biology of a Hawaiian fluviatile gastropod *Neritina granosa* (Prosobranchia: Neritidae). M.Sc. thesis, University of Hawaii
- Fowler, B.H. (1980). Reproductive biology of *Assiminea californica* (Tryon, 1865) (Mesogastropoda: Rissoacea). *The Veliger* 23: 163–166
- Franc, A. (1943). Etudes sur le développement de quelques prosobranches méditerranéens. Thesis, Université d'Alger
- Franc, A. (1968). Classe des Gastéropodes (Gastropoda Cuvier 1798). Généralités et définition. Pp. 1–39 in Grassé, P.-P. (ed.) *Traité de Zoologie*. Vol. 5 Fasc. 3. Masson et Cie: Paris
- Frank, P.W. (1969). Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. *Oecologia (Heidelberg)* 2: 232–250
- Franzén, A. (1955). Comparative morphological investigation into the spermiogenesis among Mollusca. *Zoologiska Bidrag från Uppsala* 30: 399–456
- Franzén, A. (1970). Phylogenetic aspects of the morphology of spermiogenesis. Pp. 29–46 in Baccetti, B. (ed.) *Comparative Spermatology. Proceedings of the International Symposium, Rome and Siena, 1–5 July 1969*. Academic Press: New York
- Freeman, G. & Lundelius, J.W. (1992). Evolutionary implications of the mode of D quadrant specification in coelomates with spiral cleavage. *Journal of Evolutionary Biology* 5: 205–247
- Fretter, V. (1941). The genital ducts of some British stenoglossan prosobranchs. *Journal of the Marine Biological Association of the United Kingdom* 25: 173–211
- Fretter, V. (1946). The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia*, and a discussion on their evolution in the prosobranchs. *Journal of the Marine Biological Association of the United Kingdom* 26: 312–351
- Fretter, V. (1948). The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). *Journal of the Marine Biological Association of the United Kingdom* 27: 597–632
- Fretter, V. (1951a). Some observations on the British cypraeids. *Proceedings of the Malacological Society of London* 29: 14–20
- Fretter, V. (1951b). Observations on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). *Journal of the Marine Biological Association of the United Kingdom* 29: 567–586
- Fretter, V. (1953). The transference of sperm from male to female prosobranch, with reference, also, to the pyramidellids. *Proceedings of the Linnean Society of London* 164: 217–224
- Fretter, V. (1956). The anatomy of the prosobranch *Circulus striatus* (Philippi) and a review of its systematic position. *Proceedings of the Zoological Society of London* 126: 369–381
- Fretter, V. (1964). Observations on the anatomy of *Mikadotrochus amabilis* Bayer. *Bulletin of Marine Science of the Gulf and Caribbean* 14: 172–184
- Fretter, V. (1965). Functional studies of the anatomy of some neritid prosobranchs. *Journal of Zoology, London* 147: 46–74
- Fretter, V. (1966). Biological investigations of the deep sea. 16. Observations on the anatomy of *Perotrochus*. *Bulletin of Marine Science* 16: 603–614
- Fretter, V. (1969). Aspects of metamorphosis in prosobranch gastropods. *Proceedings of the Malacological Society of London* 38: 375–386
- Fretter, V. (1972). Metamorphic changes in the velar musculature, head and shell of some prosobranch veligers. *Journal of the Marine Biological Association of the United Kingdom* 52: 161–177
- Fretter, V. (1975). *Umbonium vestiarium*, a filter-feeding trochid. *Journal of Zoology, London* 177: 541–552
- Fretter, V. (1976). The anatomy and feeding of the volutacean prosobranch *Volvarina taeniolata* Mörch. *Journal of Molluscan Studies* 42: 327–336
- Fretter, V. (1980). The evolution of some higher taxa in gastropods. Abstracts of the Symposium on the Biology and Evolution of the Mollusca, Sydney. *Journal of the Malacological Society of Australia* 4: 226–227
- Fretter, V. (1984a). The functional anatomy of the neritacean limpet *Phenacolepas omanensis* Biggs and some comparison with *Septaria*. *Journal of Molluscan Studies* 50: 8–18
- Fretter, V. (1984b). Prosobranchs. Pp. 1–45 in Tompa, A.S., Verdonk, N.H. & Biggelaar, J.A.M. van den (eds) *The Mollusca. Vol. 7. Reproduction*. Academic Press: New York
- Fretter, V. (1988). New archaeogastropod limpets from hydrothermal vents. Superfamily Lepetodrilacea. Part 2. Anatomy. *Philosophical Transactions of the Royal Society of London, Series B* 318: 33–82
- Fretter, V. (1989). The anatomy of some new archaeogastropod limpets (Superfamily Peltospiracea) from hydrothermal vents. *Journal of Zoology, London* 218: 123–169
- Fretter, V. (1990). The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. *Journal of Zoology, London* 222: 529–555
- Fretter, V. & Graham, A. (1949). The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *Journal of the Marine Biological Association of the United Kingdom* 28: 493–532

15. PROSOBRANCHS

- Fretter, V. & Graham, A. (1954). Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *Journal of the Marine Biological Association of the United Kingdom* 33: 565–585
- Fretter, V. & Graham, A. (1962) *British Prosobranch Molluscs. Their functional anatomy and ecology*. Ray Society Publications: London xvi 755 pp.
- Fretter, V. & Graham, A. (1978). The prosobranch molluscs of Britain and Denmark. Part 4. – Marine Rissoacea. *Journal of Molluscan Studies Supplement* 6: 153–241
- Fretter, V. & Graham, A. (1980). The prosobranch molluscs of Britain and Denmark. Part 5 – Marine Littorinacea. *Journal of Molluscan Studies, Supplement* 7: 243–284
- Fretter, V. & Graham, A. (1982). The prosobranch molluscs of Britain and Denmark. Part 7 – ‘Heterogastropoda’ (Cerithiopsacea, Triforacea, Epitoniacea, Eulimacea). *Journal of Molluscan Studies, Supplement* 11: 363–434
- Fretter, V. & Graham, A. (1994). *British Prosobranch Molluscs. Their functional anatomy and ecology*. Ray Society Publications: London 2nd edn xix 820 pp.
- Fretter, V., Graham, A. & McLean, J.H. (1981). The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae*. *Malacologia* 21: 337–361
- Fretter, V. & Manly, R. (1977a). The settlement and early benthic life of *Littorina neritoides* (L.) at Wembury, S. Devon. *Journal of Molluscan Studies* 43: 255–262
- Fretter, V. & Manly, R. (1977b). Algal associations of *Tricolia pullus*, *Lacuna vineta* and *Cerithiopsis tubercularis* (Gastropoda) with special reference to the settlement of their larvae. *Journal of the Marine Biological Association of the United Kingdom* 57: 999–1017
- Fretter, V. & Manly, R. (1979). Observations on the biology of some sublittoral prosobranchs. *Journal of Molluscan Studies* 45: 209–218
- Fretter, V. & Montgomery, M.C. (1968). The treatment of food by prosobranch veligers. *Journal of the Marine Biological Association of the United Kingdom* 48: 499–520
- Fretter, V. & Patil, A.M. (1958). A revision of the systematic position of the prosobranch gastropod *Cingulopsis* (= *Cingula*) *fulgida* (J. Adams). *Proceedings of the Malacological Society of London* 33: 114–126
- Fretter, V. & Pilkington, M.C. (1971). The larval shell of some prosobranch gastropods. *Journal of the Marine Biological Association of the United Kingdom* 51: 49–62
- Fritchman, H.K., III (1960). *Acmaea paradigitalis* sp. nov. (Acmaeidae, Gastropoda). *The Veliger* 2: 53–57
- Gainey, L.F. Jr (1976). Locomotion in the Gastropoda: functional morphology in the foot in *Neritina reclinata* and *Thais rustica*. *Malacologia* 15: 411–431
- Gainey, L.F. Jr & Wise, S.W. Jr (1980). Convergent shell morphology in intertidal gastropods. *Journal of Molluscan Studies* 46: 192–207
- Garrard, T.A. (1972). A review of the Australian Recent and Tertiary Turritellidae (Gastropoda: Mollusca). *Journal of the Malacological Society of Australia* 2: 267–338
- Garrard, T.A. (1961). Mollusca collected by M.V. ‘Challenge’ off the east coast of Australia. *Journal of the Malacological Society of Australia* 1(5): 3–38
- Garrard, T.A. (1963). New species of Mollusca from eastern Australia. *Journal of the Malacological Society of Australia* 1(7): 42–46
- Garrard, T.A. (1972). A revision of Australian Recent and Tertiary Turritellidae. *Journal of the Malacological Society of Australia* 2: 267–338
- Garrard, T.A. (1975). A revision of Australian Cancellariidae (Gastropoda: Mollusca). *Records of the Australian Museum* 30: 1–62
- Garrard, T.A. (1977). A revision of Australian Architectonicidae (Gastropoda: Mollusca). *Records of the Australian Museum* 31: 506–584
- Garrard, T.A. (1982). A supplement to Australian Recent Turritellidae. *Journal of the Malacological Society of Australia* 5: 195–200
- Garrity, S.D. (1984). Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65: 559–574
- Garrity, S.D. & Levings, S.C. (1981). A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. *Ecological Monographs* 51: 267–286
- Gegenbaur, C. (1855). *Untersuchungen über Pteropoden und Heteropoden. Ein beitrage zur Anatomie und Entwicklungsgeschichte dieser Thiere*. Leipzig: Leipzig vi 228 pp.
- Ghiselin, M.T. (1964). Morphological and behavioural concealing adaptations of *Lamellaria stearnsii*, a marine prosobranch gastropod. *The Veliger* 6: 123–124
- Ghiselin, M.T. & Wilson, B.R. (1965). On the anatomy, natural history, and reproduction of *Cyphoma*, a marine prosobranch gastropod. *Bulletin of Marine Science* 16: 132–142
- Giard, A. (1875). Sur l’embryogénie du *Lamellaria perspicua*. *Journal de Conchyliologie* 23: 304–346
- Giese, M. (1915). Der Genitalapparat von *Calyptrea sinensis* Linn., *Crepidula unguiformis* Lam. und *Capulus hungaricus* Lam. *Zeitschrift für Wissenschaftliche Zoologie* 114: 169–231
- Giglioli, M.E.C. (1955). The egg masses of the Naticidae (Gastropoda). *Journal of the Fisheries Research Board of Canada* 12: 287–327
- Girardi, E.-L. (1978). The Samoan land snail genus *Ostodes* (Mollusca: Prosobranchia: Poteridae). *The Veliger* 20: 191–250
- Giusti, F. (1971). L’ultrastruttura dello spermatozoo nella filogenesi e nella sistematica dei molluschi gasteropodi. *Atti della Società Italiana di Scienze Naturali e Museo Civico di Storia Naturale Milano* 112: 381–402
- Giusti, F. & Selmi, M.G. (1982a). The atypical sperm in the prosobranch molluscs. *Malacologia* 22: 171–181
- Giusti, F. & Selmi, M.G. (1982b). The morphological peculiarities of the typical spermatozoa of *Theodoxus fluviatilis* (Neritoidea) and their implications for motility. *Journal of Ultrastructure Research* 78: 166–177
- Glaser, O.C. (1907). Pathological amitosis in the food-ova of *Fasciolaria*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 13: 1–4
- Gmelin, J.F. (1791) in Linnaeus, C. *Systema Naturae* per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Emanuel Beer: Lipsiae 13th edn 3 vols in 7 pts
- Gofas, S. (1995). A remarkable species richness of the Barleeidae (Gastropoda: Rissoacea) in the Eastern Atlantic. *The Nautilus* 109: 14–37
- Gohar, H.A.F. & Eisaway, A.M. (1967). The egg-masses and development of five rachiglossan prosobranchs (from the Red Sea). *Publications of the Marine Biological Station at Al-Ghardaqa* 14: 109–147
- Gohar, H.A.F. & Soliman, G.N. (1963). On the biology of three coralliophilids boring in living corals. *Publication of the Marine Biological Station, Ghardaqa, Red Sea, Cairo* 12: 99–126
- Golikov, A.N. (1980). Buccinidae of the World Ocean. Fauna of the U.S.S.R. Mollusks 5(1). *Akademia Nauk, Leningrad* 508 pp.
- Golikov, A.N. & Kussakin, O.G. (1972). Sur la biologie de la reproduction des patelles de la famille Tecturidae (Gastropoda: Docoglossa) et sur la position systématique de ses subdivisions. *Malacologia* 11: 287–294
- Golikov, A.N. & Starobogatov, Y.I. (1975). Systematics of prosobranch gastropods. *Malacologia* 15: 185–232
- Golikov, A.N. & Starobogatov, Y.I. (1988). Problems of phylogeny and system of the prosobranchiate gastropods. USSR Academy of Sciences. *Proceedings of the Zoological Institute* 187: 4–77
- Goodwin, B.J. (1979). The egg mass of *Littorina obtusata* and *Lacuna pallidula* (Gastropoda: Prosobranchia). *Journal of Molluscan Studies* 45: 1–11
- Gosliner, T.M. (1981). Origins and relationships of primitive members of the Opisthobranchia (Mollusca: Gastropoda). *Biological Journal of the Linnean Society* 16: 197–225

- Gosliner, T.M. & Liltved, W.R. (1982). Comparative morphology of three South African Triviidae (Gastropoda: Prosobranchia) with the description of a new species. *Zoological Journal of the Linnean Society* 74 (2): 111–132
- Gosliner, T.M. & Liltved, W.R. (1985). Aspects of the morphology of the endemic South African Cypraeidae with a discussion of the evolution of the Cypraeacea and Lamellariacea. *Annals of the South African Museum* 96 (4): 67–122
- Gosliner, T.M. & Liltved, W.R. (1987). Further studies on the morphology of the Triviidae (Gastropoda: Prosobranchia) with emphasis on species from Southern Africa. *Zoological Journal of the Linnean Society* 90(3): 207–254
- Götze, E. (1938). Bau und Leben von *Caecum glabrum* (Montagu). *Zoologische Jahrbücher, Abteilung Systematik, Oekologie und Geographie der Tiere* 71: 55–122
- Gougerot, L. & Le Renard, J. (1980). Clefs de détermination des petites espèces de gastéropodes de l'éocène du Bassin Parisien. *Cahiers des Naturalistes* 35: 41–59
- Gougerot, L. & Le Renard, J. (1981). Clefs de détermination des petites espèces de gastéropodes de l'éocène du Bassin Parisien. *Cahiers des Naturalistes, neu série* 36: 17–44
- Gougerot, L. & Le Renard, J. (1982). Clefs de détermination des petites espèces de Gastéropodes de L'Eocene du Bassin Parisien. *Cahiers des Naturalistes Parisiens* 37: 29–45
- Gould, H.N. (1919). Studies on sex in the hermaphrodite mollusc, *Crepidula plana* III. Transference of the male producing stimulus through seawater. *Journal of Experimental Zoology* 29: 113–120
- Gould, H.N. (1952). Studies on sex in the hermaphrodite mollusc, *Crepidula plana* IV. Internal and external factors influencing growth and sex development. *Journal of Experimental Zoology* 119: 93–163
- Gould, S.J. (1966). Notes on shell morphology and classification of the Siliquariidae (Gastropoda). The protoconch and slit of *Siliquaria squamata* Blainville. *American Museum Novitates* No. 2263: 1–13
- Gould, S.J. (1969). Ecology and functional significance of uncoiling in *Vermicularia spirata*: an essay on gastropod form. *Bulletin of Marine Science* 19: 432–445
- Gould, S.J. (1977). *Ontogeny and Phylogeny*. Belknap Press, Harvard University: Cambridge, Massachusetts ix 501 pp.
- Gowlett-Holmes, K.L. & Holmes, N.J.C. (1989). Rediscovery of *Primovula* (P.) *heleneae* Cate and description of a new species of *Crenavolva* from South Australia (Mollusca: Gastropoda: Ovulidae). *Transactions of the Royal Society of South Australia* 113: 205–214
- Grabau, A.W. (1904). Phylogeny of *Fusus* and its allies. *Smithsonian Miscellaneous Collections* 44: 1–192
- Graham, A. (1932). On the structure and function of the alimentary system of the limpet. *Transactions of the Royal Society of Edinburgh* 57: 287–308
- Graham, A. (1938). On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proceedings of the Zoological Society of London, Series A* 108: 453–463
- Graham, A. (1939). On the structure of the alimentary canal of style-bearing prosobranchs. *Proceedings of the Zoological Society of London, Series B* 109: 75–112
- Graham, A. (1941). The oesophagus of the stenoglossan prosobranchs. *Proceedings of the Royal Society of Edinburgh, Series B* 61: 1–23
- Graham, A. (1949). The molluscan stomach. *Transactions of the Royal Society of Edinburgh* 61: 737–778
- Graham, A. (1954a). Some observations on the reproductive tract of *Ianthina janthina* (L.). *Proceedings of the Malacological Society of London* 31: 1–6
- Graham, A. (1954b). The anatomy of the prosobranch *Trichotropis borealis* Broderip and Sowerby, and the systematic position of the Capulidae. *Journal of the Marine Biological Association of the United Kingdom* 33: 19–144
- Graham, A. (1955). Molluscan diets. *Proceedings of the Malacological Society of London* 31: 144–159
- Graham, A. (1965a). The buccal mass of ianthinid prosobranchs. *Proceedings of the Malacological Society of London* 36: 323–338
- Graham, A. (1965b). Observations on the anatomy of some trochacean gastropods. *Bulletin of Marine Sciences* 15: 202–210
- Graham, A. (1966). The fore-gut of some marginellid and cancellariid prosobranchs. *Studies in Tropical Oceanography, Miami* 4: 134–151
- Graham, A. (1973). The anatomical basis of function in the buccal mass of prosobranch and amphineuran molluscs. *Journal of Zoology, London* 169: 317–348
- Graham, A. (1982). *Tornus subcarinatus* (Prosobranchia, Rissoacea), anatomy and relationships. *Journal of Molluscan Studies* 48: 144–147
- Graham, A. (1985). Evolution within the Gastropoda: Prosobranchia. Pp. 151–186 in Wilbur, K. (ed.) *Mollusca. Vol. 10. Evolution*. Academic Press: Orlando
- Grahame, J. (1977). Reproductive effort and r- and K-selection in two species of *Lacuna* (Gastropoda: Prosobranchia). *Marine Biology* 40: 217–224
- Grahame, J., Mill, P.J. & Reid, D.G. (eds) (1992). *Proceedings of the Third International Symposium on Littorinid Biology*. Malacological Society of London: London 324 pp.
- Grange, K.R. (1974). The feeding of *Tonna cerverisina* [sic]. *Poirieria* 7: 57–61
- Grant, A.R. (1937). A systematic revision of the genus *Acmaea* Eschscholtz, including consideration of ecology and speciation. PhD thesis, University of California, Zoology, Berkeley, California
- Gray, J.E. (1824). Monograph on the family Cypraeidae, a family of testaceous Mollusca. *Zoological Journal, London* 1: 71–80
- Gray, J.E. (1833). Some observations on the economy of molluscan animals, and on the structure of their shells. *Philosophical Transactions of the Royal Society of London* 1833: 771–819
- Gray, J.E. (1853). On the division of ctenobranchous gasteropodous Mollusca into larger groups and families. *Proceedings of the Zoological Society of London* 21: 32–44
- Gray, J.E. (1857). *Guide to the systematic distribution of Mollusca in the British Museum*. Pt 1. British Museum: London 230 pp.
- Greene, J.L. & Kohn, A.J. (1989). Functional morphology of the *Conus proboscis* (Mollusca: Gastropoda). *Journal of Zoology* 219: 487–493
- Grenon, J.-F. & Walker, G. (1978). The histology and histochemistry of the pedal glandular system of two limpets, *Patella vulgata* and *Acmaea tessulata* (Gastropoda: Prosobranchia). *Journal of the Marine Biological Association of the United Kingdom* 58: 803–816
- Grenon, J.-F. & Walker, G. (1981). The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology* 51: 277–308
- Grenon, J.-F. & Walker, G. (1982). Further fine structure studies of the 'space' layer which underlies the footsole epithelium of the limpet, *Patella vulgata* L. *Journal of Molluscan Studies* 48: 55–63
- Gresham, M.L. & Tracey, M. (1975). Genetic variation in an intertidal gastropod, *Collisella digitalis*. *Genetics* 80: S37
- Grobber, C. (1891). Die Pericardialdrüse der Gastropoden. *Arbeiten aus dem Zoologischen Institut der Universität Wien* 9: 35–56
- Groombridge, B. (ed.) (1994). *1994 IUCN Red List of threatened animals*. IUCN: Gland, Switzerland and Cambridge, UK. vi 286 pp.
- Gründel, J. (1975). Bemerkungen zur Familie Triforidae Jousseaume, 1884, mit Beschreibungen einiger Arten dieser Familie (Gastropoda). *Malakologische Abhandlungen* 4(16): 145–158
- Gründel, J. von. (1980). Bemerkungen zur Überfamilie Cerithiopsacea H. & A. Adams, 1854 (Gastropoda) sowie zur Fassung einiger ihrer Gattungen. *Zoologischer Anzeiger* 204: 209–264

15. PROSOBRANCHS

- Grüneberg, H. (1982). Pseudopolymorphism in *Clithron oualanensis*. *Proceedings of the Royal Society of London, Series B* 216: 147–157
- Gubbioli, F. & Nofroni, I. (1986). First record of "*Cithna naticiformis* Jeffreys, 1883 in the Mediterranean: Ecological and systematic notes. *La Conchiglia* 18 (204–205): 6–7
- Hägler, K. (1923). Anatomie von *Pachylabra (Ampullaria) cinerea* Reeve. 1 Teil. Mit Einschluss einer kurzen Besprechung der wichtigsten Literatur über die Ampullariidae. *Acta Zoologica, Stockholm* 4: 313–410
- Habe, T. (1955). Note on the systematic position of the genus *Orectospira* Dall, 1925. *Zoological Magazine, Tokyo* 64: 259–260
- Habe, T. (1961). Fauna of shell bearing mollusks of the sea around Shirikishinai, Hokkaido. 2 Gastropoda. *Fauna and Flora of the Sea around the Shirikishinai Marine Station* 3: 1–11
- Habe, T. (1962). Trichotropidae of Japan (Mollusca). *Bulletin of the National Science Museum, Tokyo* 6: 65–77
- Habe, T. (1967). A new capulid snail, *Capulus spondylicola*, from Japan. *Venus* 26: 37–38
- Habe, T. & Sato, J. (1973). A classification of the family Buccinidae from the North Pacific. *Proceedings of the Japanese Society of Systematic Zoology* 8: 1–8
- Hadfield, M.G. (1969). Nurse eggs and giant sperm in the Vermetidae. *American Zoologist* 9: 1141–1142
- Hadfield, M.G. & Hopper, C.N. (1980). Ecological and evolutionary significance of pelagic spermatophores of vermetid gastropods. *Marine Biology* 57: 315–325
- Hadfield, M.G. & Iaea, D.K. (1989). Velum of encapsulated veligers of *Petalocoelus* (Gastropoda), and the problem of re-evolution of planktotrophic larvae. *Bulletin of Marine Science* 45: 377–386
- Hadfield, M.G., Kay, E.A., Gillette, M.U. & Lloyd, M.C. (1972). The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology* 12: 81–98
- Haller, B. (1884). Untersuchungen über marine Rhipidoglossen. I. *Morphologisches Jahrbuch* 9: 1–98
- Haller, B. (1893). Die Morphologie der Prosobranchier, gesammelt auf einer Erdumsegelung durch die königl. italienische Korvette 'Vettor Pisani'. *Morphologisches Jahrbuch* 19: 553–591
- Hamner, W.M., Madin, L.P., Alldredge, A.L., Gilmer, R.W. & Hamner, P.P. (1975). Underwater observations of gelatinous zooplankton: sampling problems, feeding biology and behavior. *Limnology and Oceanography* 20: 907–917
- Hancock, D.A. (1956). The structure of the capsule and the hatching process in *Urosalpinx cinerea* (Say). *Proceedings of the Zoological Society of London* 127: 565–571
- Haneda, Y. (1958). Studies on luminescence in marine snails. *Pacific Science* 12: 152–156
- Hannaford Ellis, C. (1979). Morphology of the oviparous rough winkle, *Littorina arcana* Hannaford Ellis, 1978, with notes on the taxonomy of the *L. saxatilis* species-complex (Prosobranchia: Littorinidae). *Journal of Conchology* 30: 43–56
- Hanson, J., Randall, J.T. & Bayley, S.T. (1952). The microstructure of the spermatozoa of the snail *Viviparus*. *Experimental Cell Research* 3: 65–78
- Harasewych, M.G. (1983). A review of the Columbariinae (Gastropoda: Turbinellidae) of the western Atlantic with note on the anatomy and systematic relationships of the subfamily. *Nemouria* 27: 1–42
- Harasewych, M.G. (1984). Comparative anatomy of four primitive muricacean gastropods: implications for Trophonine phylogeny. *American Malacological Bulletin* 3(1): 11–26
- Harasewych, M.G. (1986). The Columbariinae (Gastropoda: Turbinellidae) of the eastern Indian Ocean. *Journal of the Malacological Society of Australia* 7: 155–168
- Harasewych, M.G. (1987). A revision of the genus *Benthovoluta* with notes on the evolution of the subfamily Ptychactractinae (Prosobranchia: Turbinellidae). *The Nautilus* 101: 166–181
- Harasewych, M.G. & Kantor, Y.I. (1991). *Tenebricola frigida*, new genus and species of abyssal volute from the northern Pacific Ocean (Gastropoda: Volutidae). *Nemouria* 38: 1–11
- Harasewych, M.G. & Petit, R.E. (1982). Notes on the morphology of *Cancellaria reticulata* (Gastropoda: Cancellariidae). *The Nautilus* 96: 104–113
- Harasewych, M.G. & Petit, R.E. (1984). Notes on the morphology of *Olssonella smithii* (Gastropoda: Cancellariidae). *The Nautilus* 98: 37–44
- Harasewych, M.G. & Petit, R.E. (1986). Notes on the morphology of *Admete viridula* (Gastropoda: Cancellariidae). *The Nautilus* 100: 85–91
- Harasewych, M.G. & Petit, R.E. (1989). The nomenclatural status and phylogenetic affinities of *Syrinx aruanus* Linné, 1758 (Prosobranchia: Turbinellidae). *The Nautilus* 103: 83–84
- Hardy, A. (1956). *The Open Sea. Its Natural History; part 1, the World of Plankton*. London: Collins
- Harper, J.A. & Rollins, H.B. (1982). Recognition of Monoplacophora and Gastropoda in the fossil record: a functional morphological look at the bellerophon controversy. Pp. 227–232 in Mamet, B. & Copeland, M.J. (eds) *Proceedings of the Third North American Paleontological Convention, Montreal August 5-7 1982*. Vol. 1
- Harrison, F.M. (1962). Some excretory processes in the abalone *Haliotis rufescens*. *Journal of Experimental Biology* 39: 179–192
- Haszprunar, G. (1985a). The fine morphology of the osphradial sense organs of the Mollusca. Pt 1: Gastropoda, Prosobranchia. *Philosophical Transactions of the Royal Society of London, Series B* 307: 457–496
- Haszprunar, G. (1985b). The fine morphology of the osphradial sense organs of the Mollusca. Pt 2: Allogastropoda (Architectonicidae, Pyramidellidae). *Philosophical Transactions of the Royal Society of London, Series B* 307: 497–505
- Haszprunar, G. (1985c). On the innervation of gastropod shell muscles. *Journal of Molluscan Studies* 51: 309–314
- Haszprunar, G. (1985d). The Heterobranchia – a new concept of the phylogeny and evolution of the higher Gastropoda. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 23: 15–37
- Haszprunar, G. (1985e). Zur Anatomie und systematischen Stellung der Architectonicidae (Mollusca, Allogastropoda). *Zoologica Scripta* 14: 25–43
- Haszprunar, G. (1985f). On the anatomy and systematic position of the Mathildidae (Mollusca, Allogastropoda). *Zoologica Scripta* 14: 201–213
- Haszprunar, G. (1985g). On the anatomy and fine-structure of a peculiar sense organ in *Nucula* (Bivalvia, Protobranchia). *The Veliger* 28: 52–62
- Haszprunar, G. (1987a). Anatomy and affinities of cocculinid limpets (Mollusca, Archaeogastropoda). *Zoologica Scripta* 16: 305–324
- Haszprunar, G. (1987b). The fine structure of the ctenidial sense organs (bursicles) of Vetigastropoda (Zeugobranchia, Trochoidea) and their functional and phylogenetic significance. *Journal of Molluscan Studies* 53: 46–51
- Haszprunar, G. (1987c). The anatomy of *Addisonia* (Mollusca, Gastropoda). *Zoomorphology* 106: 269–278
- Haszprunar, G. (1988a). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura (Mollusca). *Journal of Molluscan Studies* 54: 367–441
- Haszprunar, G. (1988b). A preliminary phylogenetic analysis of the streptoneurous gastropods. Pp. 7–16 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Haszprunar, G. (1988c). Comparative anatomy of cocculiniform gastropods and its bearing on archaeogastropod systematics. Pp. 64–84 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Haszprunar, G. (1988d). Anatomy and affinities of pseudococculinid limpets (Mollusca, Archaeogastropoda). *Zoologica Scripta* 17: 161–179
- Haszprunar, G. (1988e). Anatomy and systematic position of the bone-feeding limpets, *Cocculinella minutissima* (Smith) and *Osteopelta mirabilis* Marshall (Archaeogastropoda). *Journal of Molluscan Studies* 54: 1–20

- Haszprunar, G. (1988f). *Sukashitrochus* sp., a scissurellid with heteropod-like locomotion (Mollusca, Archaeogastropoda). *Annalen des Naturhistorischen Museums in Wien, Série B* 90: 367–371
- Haszprunar, G. (1989a). The anatomy of *Melanodrymia aurantiaca* Hickman, a coiled archaeogastropod from the East Pacific hydrothermal vents (Mollusca: Gastropoda). *Acta Zoologica* 70: 175–186
- Haszprunar, G. (1989b). New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Pt 2. Anatomy and relationships. *Contributions in Science, Natural History Museum of Los Angeles County* 408: 1–17
- Haszprunar, G. (1990). Towards a phylogenetic system of Gastropoda. Part 1: Traditional methodology – a reply. *Malacologia* 32: 195–202
- Haszprunar, G. (1992a). On the anatomy and relationships of the Choristellidae (Archaeogastropoda, Lepetelloidea). *The Veliger* 35: 295–307
- Haszprunar, G. (1992b). Ultrastructure of the osphradium of the Tertiary relict snail, *Campanile symbolicum* Iredale (Mollusca, Streptoneura). *Philosophical Transactions of the Royal Society of London, Series B* 337: 457–469
- Haszprunar, G. (1993). *Sententia*. The Archaeogastropoda: a clade, a grade or what else? *Bulletin of the American Malacological Union* 10: 165–177
- Haszprunar, G. & Huber, G. (1990). On the central nervous system of Smeagolidae and Rhodopidae, two families' questionably allied to the Gymnomorpha (Gastropoda: Euthyneura). *Journal of Zoology, London* 220: 185–199
- Haszprunar, G. & McLean, J.H. (1996). Anatomy and systematics of bathyphytophilid limpets (Mollusca, Archaeogastropoda) from the northeastern Pacific. *Zoologica Scripta* 25: 35–50
- Haszprunar, G., Salvini-Plawen, L. von & Rieger, R.M. (1995). Larval planktotrophy – a primitive trait in the Bilateria? *Acta Zoologica* 76: 141–154
- Hatfield, E.B. (1979). Food sources for *Anachis avara* (Columbellidae) and a discussion of feeding in the family. *The Nautilus* 93: 40–43
- Hathaway, R.E. & Woodburn, K.D. (1961). Studies on the Crown Conch *Melongena corona* Gmelin. *Bulletin of Marine Science of the Gulf and Caribbean* 11: 45–65
- Hayami, I & Kanie, Y. (1980). Mode of life of a giant capulid gastropod from the Upper Cretaceous of Saghalien and Japan. *Palaeontology* 23: 689–698
- Haynes, A. (1988). Notes on the stream neritids (Gastropoda: Prosobranchia) of Oceania. *Micronesica* 21: 93–102
- Haynes, J.A. (1990). Distribution, movement and impact of the corallivorous gastropod *Coralliophila abbreviata* (Lamarck) on a Panamanian patch reef. *Journal of Experimental Marine Biology and Ecology* 142: 25–42
- Healy, J.M. (1982a). Ultrastructure of spermiogenesis of *Philippia* (*Psilaxis*) *oxytropis* with special reference to the taxonomic position of the Architectonicidae (Gastropoda). *Zoomorphology* 101: 197–214
- Healy, J.M. (1982b). An ultrastructural examination of developing and mature euspermatozoa in *Pyrazus ebeninus* (Mollusca, Gastropoda, Potamididae). *Zoomorphology* 100: 157–175
- Healy, J.M. (1982c). Ultrastructure of paraspermatozoa, euspermatozoa and eusperm-like spermatozoa of *Obolito* cf. *fulva* (Prosobranchia: Cerithiacea). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 35: 489–500
- Healy, J.M. (1983). Ultrastructure of euspermatozoa of cerithiacean gastropods (Prosobranchia: Mesogastropoda). *Journal of Morphology* 178: 57–75
- Healy, J.M. (1984). The ultrastructure of gastropod spermatozoa and spermiogenesis. Unpublished PhD thesis, University of Queensland, Brisbane
- Healy, J.M. (1986a). Ultrastructure of paraspermatozoa of cerithiacean gastropods (Prosobranchia: Mesogastropoda). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 40: 177–199
- Healy, J.M. (1986b). Euspermatozoa and paraspermatozoa of the relict cerithiacean gastropod, *Campanile symbolicum* (Prosobranchia, Mesogastropoda). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 40: 201–218
- Healy, J.M. (1988a). Sperm morphology and its systematic importance in the Gastropoda. Pp. 251–266 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Healy, J.M. (1988b). Sperm morphology in *Serpulorbis* and *Dendropoma* and its relevance to the systematic position of the Vermetidae (Gastropoda). *Journal of Molluscan Studies* 54: 295–308
- Healy, J.M. (1990a). Euspermatozoa and paraspermatozoa in the trochid gastropod *Zalipais laseroni* (Trochoidea: Skeneidae). *Marine Biology* 105: 497–507
- Healy, J.M. (1990b). Systematic importance of spermatzeugmata in triphorid and cerithiospid gastropods (Triphoroidea, Caenogastropoda). *Journal of Molluscan Studies* 56: 115–118
- Healy, J.M. (1990c). Sperm structure in the scissurellid gastropod *Sinezona* sp. (Prosobranchia, Pleurotomarioidea). *Zoologica Scripta* 19: 189–193
- Healy, J.M. (1990d). Taxonomic affinities of the deep-sea gastropod genus *Provanna*: new evidence from sperm ultrastructure. *Journal of Molluscan Studies* 56: 119–122
- Healy, J.M. (1990e). Spermatozoa and spermiogenesis of *Cornirostra*, *Valvata* and *Orbitestella* (Gastropoda: Heterobranchia): with a discussion of valvatoidean sperm morphology. *Journal of Molluscan Studies* 56: 557–566
- Healy, J.M. (1991). Sperm morphology in the marine gastropod *Architectonica perspectiva* (Mollusca): unique features and systematic relevance. *Marine Biology* 109: 59–65
- Healy, J.M. (1993a). Comparative sperm ultrastructure and spermiogenesis in basal heterobranch gastropods (Valvatoidea, Architectonicoidea, Rissoelloidea, Omalogyroidea, Pyramidelloidea) (Mollusca). *Zoologica Scripta* 22: 63–276
- Healy, J.M. (1993b). Transfer of the gastropod family Plesiotrochidae to the Campaniloidea based on sperm ultrastructural evidence. *Journal of Molluscan Studies* 59: 135–146
- Healy, J.M. (1995). Sperm and spermiogenic ultrastructure in the Mathildidae with a review of sperm morphology and its systematic importance in the Architectonicoidea (Gastropoda, Mollusca). *Journal of Molluscan Studies* 61: 361–373
- Healy, J.M. (1996). Molluscan sperm ultrastructure: correlation with taxonomic units within the Gastropoda, Cephalopoda and Bivalvia. Pp. 99–113 in Taylor, J. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Healy, J.M. & Jamieson, B.G.M. (1981). An ultrastructural examination of developing and mature paraspermatozoa in *Pyrazus ebeninus* (Mollusca, Gastropoda, Potamididae). *Zoomorphology* 98: 101–119
- Healy, J.M. & Jamieson, B.G.M. (1991). Ultrastructure of spermiogenesis in the gastropod *Heliacus variegatus* (Architectonicoidea) with description of a banded, periaxonemal helix. *Marine Biology* 109: 67–77
- Hedegaard, C. (1990). Shell structures of the Recent Archaeogastropoda. Candian Science thesis, Department of Ecology and Genetics, University of Aarhus, Denmark 2 vols, 154 pp. atlas 78 pls
- Hedegaard, C., Bandel, K. & Lindberg, D.R. (in press). A patello-gastropod limpet from the St. Cassian Formation of Triassic Italy. *Lethaia*
- Hedley, C. (1901). Studies on Australian Mollusca. Part III. *Proceedings of the Linnean Society* 25 (1900): 721–732
- Hedley, C. (1903). Scientific results of the trawling expedition of H.M.C.S. Thetis, off the coast of New South Wales, in February and March, 1898. Mollusca. Part 2, Scaphopoda and Gastropoda. *Australian Museum Memoir* 4: 327–402
- Hedley, C. (1905). Studies on Australian Mollusca. Part IX. *Proceedings of the Linnean Society of New South Wales* 30: 520–546
- Hedley, C. (1907). The Mollusca of Masthead Reef, Capricorn Group, Queensland. *Proceedings of the Linnean Society of New South Wales* 32: 476–513

- Hedley, C. (1910a). *Papers and Proceedings of the Royal Society of Tasmania* 1910: Pl. 25, No. 23
- Hedley, C. (1910b). The marine Mollusca of Queensland. *Report of the Australian Association for the Advancement of Science* 12: 329–371, Addendum 809–810
- Hedley, C. (1916). A preliminary index of the Mollusca of Western Australia. *Journal and Proceedings of the Royal Society of Western Australia* 1: 155–226
- Hedley, C. (1917). Studies on Australian Mollusca. Pt XIII. *Proceedings of the Linnean Society of New South Wales* 41: 680–719 [1916]
- Hedley, C. (1922). A revision of the Australian Turridae. *Records of the Australian Museum* 13: 213–359
- Heller, J. (1975). The taxonomy of some British *Littorina* species, with notes on their reproduction (Mollusca: Prosobranchia). *Zoological Journal of the Linnean Society of London* 56: 131–151
- Henderson, G. (1986). *Maritime Archaeology in Australia*. University of Western Australia Press : Nedlands, Western Australia ix 201 pp.
- Hendler, G. & Franz, D.R. (1971). Population dynamics and life history of *Crepidula convexa* Say (Gastropoda: Prosobranchia) in Delaware Bay. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 141: 514–526
- Herbert, D.G. (1984). Some aspects of the fine structure of the sense organs and endocrine system of archaeogastropods. Unpublished thesis, University of London : London
- Herbert, D.G. (1986). A revision of the southern African Scissurellidae (Mollusca: Gastropoda: Prosobranchia). *Annals of the Natal Museum* 27: 601–632
- Herbert, D.G. (1987a). Taxonomic studies on the Emarginulinae (Mollusca: Gastropoda: Fissurellidae) of southern Africa and Mozambique. *Hemitoma, Clypidina, Tugali, Scutus, Zeidora* and two species of *Emarginula*. *South African Journal of Zoology* 22: 1–13
- Herbert, D.G. (1987b). Revision of the Solariellinae (Mollusca: Prosobranchia: Trochidae) in southern Africa. *Annals of the Natal Museum* 28: 283–382
- Herbert, D.G. (1988). Observations on the southern African fissurellids *Cosmetalepas africana* and *Macroschisma africana* (Mollusca: Gastropoda: Fissurellidae). *Annals of the Natal Museum* 29: 491–501
- Herbert, D.G. (1992). Revision of the Umboniinae (Mollusca: Prosobranchia: Trochidae) in southern Africa and Mozambique. *Annals of the Natal Museum* 33: 379–459
- Herbert, D.G. & Kilburn, R.N. (1985). Taxonomic studies on the Emarginulinae (Mollusca: Gastropoda: Fissurellidae) of southern Africa and Mozambique. *Emarginula, Emarginella, Puncturella, Fissurisepta* and *Rimula*. *South African Journal of Zoology* 21: 1–27
- Hertling, H. (1928). Beobachtungen und Versuche an den Eiern von *Littorina* und *Lacuna*. Bedeutung der Eihüllen. Entwicklung im natürlichen und abgeänderten Medium. *Wissenschaftliche Meeresuntersuchungen, Abteilung Helgoländer* 17: 1–49
- Hesse, K.O. (1979). Movement and migration of the queen conch, *Strombus gigas*, in the Turks and Caicos Islands. *Bulletin of Marine Science* 29: 303–311
- Hickman, C.S. (1976). *Pleurotomaria* (Archaeogastropoda) in the Eocene of the northeastern Pacific: a review of Cenozoic biogeography and ecology of the genus. *Journal of Paleontology* 50: 1090–1102
- Hickman, C.S. (1980). Gastropod radulae and the assessment of form in evolutionary paleontology. *Paleobiology* 6: 276–294
- Hickman, C.S. (1981a). Evolution and function of asymmetry in the archaeogastropod radula. *The Veliger* 23: 189–194
- Hickman, C.S. (1981b). Selective deposit feeding by the deep-sea archaeogastropod *Bathybembix aeola*. *Marine Ecology Progress Series* 6: 339–342
- Hickman, C.S. (1983). Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *The Veliger* 26: 73–92
- Hickman, C.S. (1984a). *Pleurotomaria*: pedigreed perseverance? Pp. 225–231 in Eldredge, N. & Stanley, S.M. (eds) *Living Fossils*. Springer-Verlag : Berlin
- Hickman, C.S. (1984b). Form and function of the radulae of pleurotomariid gastropods. *The Veliger* 27: 29–36
- Hickman, C.S. (1984c). Implications of radular tooth-row functional integration for archaeogastropod systematics. *Malacologia* 25: 143–160
- Hickman, C.S. (1985). Comparative morphology and ecology of free-living suspension feeding gastropods from Hong Kong. Pp. 217–234 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and Southern China 2. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 6–24 April 1983*. Hong Kong University Press : Hong Kong
- Hickman, C.S. (1988). Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. Pp. 17–34 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Hickman, C.S. (1992). Reproduction and development of trochacean gastropods. *The Veliger* 35: 245–272
- Hickman, C.S. (1995). Phylogeny and patterns of evolutionary radiation in trochoidean gastropods. Pp. 177–198 in Taylor, J.D. *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Hickman, C.S. & Lindberg, D.R. (1985). Perspectives on molluscan phylogeny. Pp. 13–16 in Broadhead, T.W. (ed.) *Mollusks. Notes for a Short Course*. University of Tennessee, Department of Geological Science, Studies in Geology No. 13
- Hickman, C.S. & McLean, J.H. (1990). Systematic revision and suprageneric classification of trochacean gastropods. *Science Series, Natural History Museum of Los Angeles County* 35: 1–169
- Hickman, C.S. & Morris, T.E. (1985). Gastropod feeding tracks as a source of data in analysis of the functional morphology of radulae. *The Veliger* 27: 357–365
- Hidalgo, R.J. (1906–1907). Monografía de las especies vivientes del género *Cypraea*. *Memorias de la Real Academia de Ciencias Exactas, Físicas y Naturales de Madrid* 15: 1–588
- Hinton, A. (1978). *Guide to Australian Shells*. Robert Brown & Associates : Port Moresby 77 pls.
- Hoagland, K.E. (1977). Systematic review of fossil and Recent *Crepidula* and discussion of evolution of the Calyptraeidae. *Malacologia* 16: 353–420
- Hoagland, K.E. (1978). Protandry and the evolution of environmentally-mediated sex change: a study of the Mollusca. *Malacologia* 17: 365–391
- Hoagland, K.E. (1983). Ecology and larval development of *Crepidula protea* (Prosobranchia: Crepidulidae) from southern Brasil: a new type of egg capsule for the genus. *The Nautilus* 97: 105–109
- Hoagland, K.E. (1984a). Aerial exposure in the genus *Crepidula* (Gastropoda: Prosobranchia) with comparisons to other taxa. *American Malacological Bulletin* 3: 33–40
- Hoagland, K.E. (1984b). Use of molecular genetics to distinguish species of the gastropod genus *Crepidula* (Prosobranchia: Calyptraeidae). *Malacologia* 25: 607–628
- Hoagland, K.E. (1986). Patterns of encapsulation and brooding in the Calyptraeidae (Prosobranchia: Mesogastropoda). *American Malacological Bulletin* 4: 173–183
- Hoagland, K.E. & Davis, G.M. (1979). The stenothyrid radiation of the Mekong River. 1. The *Stenothyra mcmulleni* complex (Gastropoda: Prosobranchia). *Proceedings of the Academy of Natural Sciences of Philadelphia* 131: 191–230
- Hochpöchler, F. (1981). Die postembryonale Entwicklung des weiblichen Geschlechtsapparates von *Neritina punctulata* (Gastropoda, Prosobranchia, Neritacea). *Zoologischer Anzeiger* 206: 49–56
- Hockey, P.A.R. & Bosman, A.L. (1986). Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* 46: 3–14
- Hodgson, A.N. & Bernard, R.T.F. (1988). A comparison of the structure of spermatozoa and spermatogenesis for 16 species of patellid limpet (Mollusca: Gastropoda: Archaeogastropoda). *Journal of Morphology* 195: 205–223

- Hodgson, A.N. & Bernard, R.T.F. (1988). A comparison of the structure of spermatozoa and spermatogenesis of 16 species of patellid limpet (Mollusca: Gastropoda: Archaeogastropoda). *Journal of Morphology* 195: 205–223
- Hodgson, A.N. & Chia, F.-S. (1993). Spermatozoon structure of some North American prosobranchs from the families Lottiidae (Patellogastropoda) and Fissurellidae (Archaeogastropoda). *Marine Biology* 116: 97–101
- Hodgson, A.N. & Foster, G.G. (1992). Structure of the sperm of some South African archaeogastropods (Mollusca) from the superfamilies Haliotoidea, Fissurelloidea and Trochoidea. *Marine Biology* 113: 89–97
- Hodgson, A.N. & Heller, J. (1990). Spermatogenesis and sperm structure of the normally parthenogenetic freshwater snail *Melanoides tuberculata*. *Israel Journal of Zoology* 37: 31–50
- Hoerle, R.C. (1974). A recent Caribbean species of the genus *Neritopsis* (Mollusca: Gastropoda). *Tulane Studies in Geology and Palaeontology* 11: 103–104
- Hoffman, D.L., Homan, W.C., Swanson, J. & Weldon, P.J. (1978). Flight responses of three congeneric species of intertidal gastropods (Prosobranchia: Neritidae) to sympatric predatory gastropods from Barbados. *The Veliger* 21: 293–296
- Hollister, S.C. (1954). Some notes on the radula. *The Nautilus* 68: 44–46
- Hollister, S.C. (1958). A review of the genus *Busycon* and its allies. *Palaeontographica Americana* 4: 47–126
- Hori, S. & Tsuchida, E. (1995). A revision of the systematic position of the genus *Leucotina* (Gastropoda: Heterostrophia). *Venus* 54: 279–293
- Hornell, J. (1951). *Indian Molluscs*. Bombay Natural History Society: Bombay iv 96 pp. 1 pl.
- Houart, R. (1992). The genus *Chicoreus* and related genera (Gastropoda: Muricidae) in the Indo-West Pacific. *Mémoires du Muséum National d'Histoire Naturelle, Série A Zoologie* 154: 1–188
- Houbrick, R.S. (1971). Some aspects of the anatomy, reproduction, and early development of *Cerithium nodulosum* (Bruguère) (Gastropoda, Prosobranchia). *Pacific Science* 25: 560–565
- Houbrick, R.S. (1973). Studies in the reproductive biology of the genus *Cerithium* (Gastropoda: Prosobranchia) in the Western Atlantic. *Bulletin of Marine Science* 23: 875–904
- Houbrick, R.S. (1974). Growth studies on the genus *Cerithium* (Gastropoda: Prosobranchia) with notes on ecology and microhabitats. *The Nautilus* 88: 14–27
- Houbrick, R.S. (1976a). Preliminary revision of supraspecific taxa in the Cerithiinae Fleming, 1822 (Cerithiidae: Prosobranchia). *Bulletin of the American Malacological Union* 1975: 14–18
- Houbrick, R.S. (1976b). The family Cerithiidae in the Indo-Pacific. Part I. The genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium*. *Monographs of Marine Mollusca* 1: 1–130
- Houbrick, R.S. (1977). Reevaluation and new description of the genus *Bittium* (Cerithiidae). *The Veliger* 20: 101–106
- Houbrick, R.S. (1980a). Observations on the anatomy and life history of *Modulus modiolus* (Prosobranchia: Modulidae). *Malacologia* 20: 117–142
- Houbrick, R.S. (1980b). Review of the deep-sea genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae). *Smithsonian Contributions to Zoology* 321: 1–30
- Houbrick, R.S. (1980c). Reappraisal of the gastropod genus *Varicopeza* Gründel (Cerithiidae: Prosobranchia). *Proceedings of the Biological Society of Washington* 93: 525–535
- Houbrick, R.S. (1980d). Form, function and adaptive radiation in the Cerithiidae. *Journal of the Malacological Society of Australia* 4: 230–231
- Houbrick, R.S. (1981a). Anatomy, biology and systematics of *Campanile symbolicum* with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia). *Malacologia* 21: 263–289
- Houbrick, R.S. (1981b). Anatomy and systematics of *Gourmya gourmyi* (Prosobranchia: Cerithiidae), a Tethyan relict from the southwest Pacific. *The Nautilus* 95: 2–11
- Houbrick, R.S. (1981c). Anatomy of *Diastoma melanioides* (Reeve, 1849) with remarks on the systematic position of the family Diastomatidae (Prosobranchia: Gastropoda). *Proceedings of the Biological Society of Washington* 94: 598–621
- Houbrick, R.S. (1981d). Systematic position of the genus *Glyptozaria* Iredale (Prosobranchia: Gastropoda). *Proceedings of the Biological Society of Washington* 94: 838–847
- Houbrick, R.S. (1984a). *Diastoma melanioides* (Reeve), a relict snail from South Australia. Pp. 236–239 in Eldridge, N. & Stanley, S. (eds) *Living Fossils*. Springer Verlag: Berlin
- Houbrick, R.S. (1984b). The relict cerithiid prosobranch *Gourmya gourmyi* (Crosse). Pp. 240–242 in Eldridge, N. & Stanley, S. (eds) *Living Fossils*. Springer Verlag: Berlin
- Houbrick, R.S. (1984c). Revision of higher taxa in genus *Cerithidea* (Mesogastropoda: Potamididae) based on comparative morphology and biological data. *American Malacological Bulletin* 2: 1–20
- Houbrick, R.S. (1984d). The giant creeper, *Campanile symbolicum* Iredale, an Australian relict marine snail. Pp. 232–235 in Eldridge, N. & Stanley, S. (eds) *Living Fossils*. Springer Verlag: Berlin
- Houbrick, R.S. (1985). Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology* 403: 1–131
- Houbrick, R.S. (1986a). The systematic position of *Royella sinon* (Bayle) (Prosobranchia: Cerithiidae). *The Veliger* 28: 429–435
- Houbrick, R.S. (1986b). *Cerithidea reidi*, spec. nov., from Western Australia. *The Veliger* 28: 280–286
- Houbrick, R.S. (1986c). Discovery of a new living *Cerithioclava* species in the Caribbean (Mollusca: Prosobranchia: Cerithiidae). *Proceedings of the Biological Society of Washington* 99: 257–260
- Houbrick, R.S. (1987a). Anatomy, reproductive biology, and phylogeny of the Planaxidae (Cerithiacea: Prosobranchia). *Smithsonian Contributions to Zoology* 445: 1–57
- Houbrick, R.S. (1987b). Anatomy of *Alaba* and *Litiopa* (Prosobranchia: Litiopidae): Systematic implications. *The Nautilus* 101: 9–18
- Houbrick, R.S. (1987c). Anatomy and systematic position of *Fastigiella carinata* Reeve (Cerithiidae: Prosobranchia). *The Nautilus* 101: 101–110
- Houbrick, R.S. (1987d). Description of a new, giant *Ataxocerithium* species from Australia with remarks on the systematic placement of the genus (Prosobranchia: Cerithiopsidae). *Nautilus* 101: 155–161
- Houbrick, R.S. (1988). Cerithioidean phylogeny. Pp. 88–128 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement* 4
- Houbrick, R.S. (1989). *Campanile* revisited: implications for cerithioidean phylogeny. *American Malacological Bulletin* 7: 1–6
- Houbrick, R.S. (1990a). Anatomy, reproductive biology and systematic position of *Fossarus ambiguus* (Linné) (Fossarinae: Planaxidae; Prosobranchia). *Açoreana, Suplemento* 1990: 59–73
- Houbrick, R.S. (1990b). Aspects of the anatomy of *Plesiotrochus* (Plesiotrochidae fam. n.) and its systematic position in Cerithioidea (Prosobranchia, Caenogastropoda). Pp. 237–249 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. *Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia*. Vol. 2. Western Australian Museum: Perth
- Houbrick, R.S. (1990c). Review of the genus *Colina* H. and A. Adams, 1854 (Cerithiidae: Prosobranchia). *The Nautilus* 104: 35–52
- Houbrick, R.S. (1991). Systematic review and functional morphology of the mangrove snails *Terebralia* and *Telescopium* (Potamididae; Prosobranchia). *Malacologia* 33: 289–338
- Houbrick, R.S. (1992a). Monograph of the genus *Cerithium* Bruguère in the Indo-Pacific (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology* 510: 1–211

15. PROSOBRANCHS

- Houbrick, R.S. (1992b). *Simulathena papuensis*, a new planaxid genus and species from the Indo-West Pacific. *The Veliger* 35: 64–69
- Houbrick, R.S. (1993a). Phylogenetic relationships and generic review of the Bittiinae (Prosobranchia: Cerithioidea). *Malacologia* 35: 261–313
- Houbrick, R.S. (1993b). Two confusing Indo-Pacific cerithiids. *The Nautilus* 107: 14–23
- Houbrick, H.S. & Fretter, V. (1969). Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. *Proceedings of the Malacological Society of London* 38: 415–429
- Houlihan, D.F., Innes, A.J. & Dey, D.G. (1981). The influence of mantle cavity fluid on the aerial oxygen consumption of some intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* 49: 57–68
- Houston, R.S. (1976). The structure and function of neogastropod reproductive systems: with special reference to *Columbella fuscata* Sowerby, 1832. *The Veliger* 19: 27–46
- Houston, R.S. (1985). Genital ducts in the Cerithiacea (Gastropoda: Mesogastropoda) from the Gulf of California. *Journal of Molluscan Studies* 51: 183–189
- Houston, R.S. (1990). Reproductive systems of neritimorph archaeogastropods from the eastern Pacific, with special reference to *Nerita funiculata* Menke, 1851. *The Veliger* 33: 103–110
- Houston, R.S. & Hatfield, E.B. (1981). The reproductive system of the Western Atlantic *Anarchis avara* (Gastropoda: Columbellidae). *The Nautilus* 95: 136–139
- Hubendick, B. (1952). Notes on the genus *Fluviopupa*, with descriptions of two new species. *Occasional Papers of the Bernice P. Bishop Museum* 20: 289–296
- Huber, G. (1993). On the central nervous system of marine Heterobranchia (Gastropoda). *Journal of Molluscan Studies* 59: 381–420
- Hughes, H.P.I. (1993). *Parastrophia* from Rottnest Island, Western Australia (Gastropoda: Caecidae). Pp. 183–192 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *The Marine Flora and Fauna of Rottnest Island, Western Australia*. Western Australian Museum : Perth
- Hughes, J.M. & Mather, P.B. (1986). Evidence for predation as a factor in determining shell color frequencies in a mangrove snail *Littorina* sp. (Prosobranchia: Littorinidae). *Evolution* 40: 68–77
- Hughes, R.N. (1978). The biology of *Dendropoma corralinaceum* and *Serpulorbis natalensis*, two South African vermetid gastropods. *Zoological Journal of the Linnean Society* 64: 111–127
- Hughes, R.N. (1979). Coloniality in Vermetidae (Gastropoda). Pp. 243–253 in Larwood, G. & Rosen, B.R. (eds) *Biology and Systematics of Colonial Organisms*. Systematic Association Special, Vol. 11. Academic Press : London
- Hughes, R.N. (1985a). Feeding behaviour of the sessile gastropods *Vermicularia pellucida* and *Stephopoma pennatulium* (Turritellidae, Vermiculariinae). *Journal of Molluscan Studies* 51: 320–325
- Hughes, R.N. (1985b). Feeding behaviour of the sessile gastropod *Tripsyche tulipa* (Vermetidae). *Journal of Molluscan Studies* 51: 326–330
- Hughes, R.N. (1985c). Notes on the feeding behaviour of *Tonna zonatum* (Tonnidae) and *Phalium bisulcatum* (Cassidae) (Tonnacea). Pp. 623–626 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and southern China 2. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 6–24 April 1983*. Hong Kong University Press : Hong Kong
- Hughes, R.N. (1986). Anatomy of the foregut of *Morum* Röding, 1798 (Gastropoda: Tonnacea) and the taxonomic misplacement of the genus. *The Veliger* 29: 91–100
- Hughes, R.N. (1990). Larval development of *Morum oniscus* (L.) (Gastropoda: Harpidae). *Journal of Molluscan Studies* 56: 1–8
- Hughes, R.N. (1993). The vermetid gastropods of Rottnest Island, Western Australia. Pp. 193–205 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia*. Vol. 1. Western Australian Museum : Perth
- Hughes, R.N. & Emerson, W.K. (1987). Anatomical and taxonomic characteristics of *Harpa* and *Morum* (Neogastropoda: Harpidae). *The Veliger* 29: 349–358
- Hughes, R.N. & Hughes, H.P.I. (1971). A study of the gastropod *Cassia tuberosa* (L.) preying upon sea urchins. *Journal of Experimental Marine Biology and Ecology* 7: 305–314
- Hughes, R.N. & Hughes, H.P.I. (1981). Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). *Malacologia* 20: 385–402
- Hughes, R.N. & Hughes, H.P.I. (1987). Spawning and hatching of *Cypraeacassis testiculus* Linnaeus, 1758 (Tonnacea: Cassidae). *The Veliger* 29: 256–259
- Hughes, R.N. & Lewis, A.H. (1974). On the spatial distribution, feeding and reproduction of the vermetid gastropod *Dendropoma maximum*. *Journal of Zoology, London* 172: 531–574
- Hultin, T. (1948). On the question of sperm-antifertilizin. *Pubblicazioni della Stazione Zoologica di Napoli* 21: 153–163
- Hunter, W.R. (1957). Studies on freshwater snails at Loch Lomond. *Glasgow University Publication Studies Loch Lomond* 1: 56–95
- Hyman, L.H. (1967). *The Invertebrates*. Vol. VI Mollusca I. McGraw-Hill : New York vii 792 pp.
- ICZN (1992). Opinion 1664. Rissoidae Gray, 1847 (Mollusca, Gastropoda): given precedence over Truncatellidae Gray, 1840. *Bulletin of Zoological Nomenclature* 49: 78–80
- Ino, T. (1952). Biological studies on the propagation of Japanese abalone (genus *Haliotis*). *Bulletin of Tokai Regional Fisheries Research Laboratory* 5: 1–102 [in Japanese with English summary; English translation by T. Kanaya, Stanford University 1954, mimeographed, 114 pp.]
- Ino, T. (1953). Ecological studies of *Turbo cornutus* Solander – I. Changes of the spines on the shell due to environments. *Bulletin of the Japanese Society of Scientific Fisheries* 19: 410–414
- Iredale, T. (1915). A commentary on Suter's "Manual of the New Zealand Mollusca". *Transactions of the New Zealand Institute* 47: 417–497
- Iredale, T. (1917a). On some new species of marine Mollusca from Christmas Island, Indian Ocean. *Proceedings of the Malacological Society of London* 12: 331–334
- Iredale, T. (1917b). More molluscan name-changes, generic and specific. *Proceedings of the Malacological Society of London* 12: 322–330
- Iredale, T. (1924). Results from Roy Bell's molluscan collections. *Proceedings of the Linnean Society of New South Wales* 49: 179–278
- Iredale, T. (1927). A review of Australian helmet shells (Family Cassididae – Phylum Mollusca). *Records of the Australian Museum* 15: 321–354
- Iredale, T. (1929a). Queensland molluscan notes, No. 1. *Memoirs of the Queensland Museum* 9: 261–297
- Iredale, T. (1929b). Mollusca from the continental shelf of Eastern Australia. No. 2. *Records of the Australian Museum* 17: 157–189
- Iredale, T. (1930). Queensland Molluscan Notes, No. 2. *Memoirs of the Queensland Museum* 10(1): 73–88
- Iredale, T. (1931). Australian molluscan notes, No. 1. *Records of the Australian Museum* 18: 201–235
- Iredale, T. (1933). Systematic notes on Australian land shells. *Records of the Australian Museum* 19: 37–59
- Iredale, T. (1935). Australian Cowries. Pt I. *Australian Zoologist* 8(2): 96–135
- Iredale, T. (1936a). Australian molluscan notes, No. 2. *Records of the Australian Museum* 19: 267–340
- Iredale, T. (1936b). Australian Cowries. Pt II. *Australian Zoologist* 9: 297–323
- Iredale, T. (1937a). A basic list of the land Mollusca of Australia. *Australian Zoologist* 8: 287–333

- Iredale, T. (1937b). Mollusca. In Whitley, G.P. (ed.) *The Middleton and Elizabeth Reefs South Pacific Ocean*. Australian Zoologist 8: 232–263
- Iredale, T. (1938). A new name for an old shell. *Australian Zoologist* 9: 172
- Iredale, T. (1943). A basic list of the fresh water Mollusca of Australia. *Australian Zoologist* 10(2): 188–230
- Iredale, T. (1944). The land Mollusca of Lord Howe Island. *Australian Zoology* 10: 299–334
- Iredale, T. (1945). The land Mollusca of Norfolk Island. *Australian Zoologist* 11: 46–71
- Iredale, T. (1957). An exciting find. *Proceedings of the Royal Society of New South Wales* 1955–56 [1957]: 124–125
- Iredale, T. & Allan, J. (1940). A review of the relationships of the Mollusca of Lord Howe Island. *Australian Zoologist* 9: 444–451
- Iredale, T. & Laseyron, C.F. (1957). The systematic status of *Citloceras* and some comparative genera. *Proceedings of the Royal Zoological Society of New South Wales* 1955–56 [1957]: 97–109
- Iredale, T. & McMichael, D.F. (1962). A reference list of marine Mollusca of New South Wales. *Memoirs of the Australian Museum* 11: 1–109
- Ivanov, A.V. (1945). A new endoparasitic mollusc, *Parenteroxenos dogieli*, nov. gen., nov. sp. *Proceedings of the USSR Academy of Sciences, Biological Series* 48: 450–452 [in Russian]
- Iversen, E.S., Rutherford, E.S., Bannerot, S.P. & Jory, D.E. (1987). Biological data on Berry Islands (Bahamas) queen conchs, *Strombus gigas*, with mariculture and fisheries management implications. *Fisheries Bulletin* 85: 299–310
- Iwasaki, K. (1992). Factors affecting individual variation in resting site fidelity in the patellid limpet, *Cellana toreuma* (Reeve). *Ecological Research* 7: 305–331
- Jacob, J. (1957). Cytological studies of Melaniidae (Mollusca) with special reference to parthenogenesis and polyploidy. I. Oögenesis of the parthenogenetic species of 'Melanoides' (Prosobranchia–Gastropoda). *Transactions of the Royal Society of Edinburgh* 63: 341–352
- Jacob, J. (1958). Cytological studies of Melaniidae (Mollusca) with special reference to parthenogenesis and polyploidy. II. A study of meiosis in the rare males of the polyploid race of 'Melanoides tuberculatus' and *Melanoides lineatus*. *Transactions of the Royal Society of Edinburgh* 83: 433–444
- Jamieson, B.G.M., Hodgson, A.N. & Benard, R.T.F. (1991). Phylogenetic trends and variation in the ultrastructure of the spermatozoa of sympatric species of South African patellid limpets (Archaeogastropoda, Mollusca). *Invertebrate Reproduction and Development* 20: 137–146
- Jamieson, B.J.M. & Newman, L.J. (1989). The phylogenetic position of the heteropod *Atlanta gaudichaudi* Souleyet, 1852 (Gastropoda: Mollusca), a spermatological investigation. *Zoologica Scripta* 18: 269–278
- Jansen, P. (1994a). Notes on the Australian species of *Calliotropis* (Gastropoda: Trochidae) with descriptions of four new species. *Molluscan Research* 15: 43–53
- Jansen, P. (1994b). Notes on the Australian species of *Euchelus* and *Herpetopoma* (Gastropoda: Trochidae) with descriptions of new species. *Molluscan Research* 15: 55–66
- Jeffreys, J.G. (1883). On the Mollusca procured during the 'Lightning' and 'Porcupine' expeditions, 1868–1870. (Part VI). *Proceedings of the Zoological Society of London* 1883: 88–115
- Jenkins, B.W. (1984a). Southern Australian Liotiidae. *Australian Shell News* 47: 3–5
- Jenkins, B.W. (1984b). Northern Australian Liotiidae. *Australian Shell News* 48: 8–9
- Jenner, M.G. (1979). Pseudohermaphroditism in *Ilyanassa obsoleta* (Mollusca: Neogastropoda). *Science* 205: 1407–1409
- Jensen, K.T. & Siegismund, H.R. (1980). The importance of diatoms and bacteria in the diet of *Hydrobia*-species. *Ophelia, Supplement* 1: 193–199
- Jernakoff, P. (1985a). An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on the algal diversity and cover in an intertidal barnacle zone. *Journal of Experimental Marine Biology and Ecology* 88: 287–302
- Jernakoff, P. (1985b). Interactions between the limpet *Patelloida latistrigata* and algae on an intertidal rock-platform. *Marine Ecology Progress Series* 23: 71–78
- Johannesson, K., Raffaelli, D.G. & Hannaford Ellis, C.J. (eds) (1990). Progress in littorinid and muricid biology. [Proceedings of the Second European Meeting on Littorinid Biology, Tjärnö Marine Biological Laboratory, Sweden, July 4–8, 1988]. *Hydrobiologia* 193: 1–273
- Johansson, J. (1950). On the embryology of *Viviparus* and its significance for the phylogeny of the Gastropoda. *Arkiv för Zoologi* 1: 173–177
- Johansson, J. (1953). On the genital organs of some mesogastropods: *Cerithium vulgatum* Brug., *Triphora perversa* (L.), and *Melanella (Eulima) intermedia* (Cantr.). Pp. 1–23 in *Contributions to the Phylogeny of the Pallial Gonoducts of the Prosobranchia*. Zoologiska Bidrag från Uppsala 30
- Johnson, M.S. & Black, R. (1991). Genetic subdivision of the intertidal snail *Bembicium vittatum* (Gastropoda: Littorinidae) varies with habitat in the Houtman Abrolhos Islands, Western Australia. *Heredity* 67: 205–213
- Johnson, M.S. & Black, R. (1995). Neighbourhood size and the importance of barriers to gene flow in an intertidal snail. *Heredity* 75: 142–154
- Johnson, M.S. & Black, R. (1996). Geographic cohesiveness versus associations with habitat: genetic subdivision of *Bembicium vittatum* Philippi (Gastropoda: Littorinidae) in the Houtman Abrolhos Islands. *Biological Journal of the Linnean Society* 58: 57–74
- Johnson, M.S. & Cumming, R.L. (1995). Genetic distinctiveness of three widespread and morphologically variable species of *Drupella* (Gastropoda: Muricidae). *Coral Reefs* 14: 71–78
- Joll, L.M. (1980). Reproductive biology of two species of Turbinidae (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 31: 319–336
- Jones, H.D. (1984). Shell cleaning behaviour of *Calliostoma zizyphinum*. *Journal of Molluscan Studies* 50: 245–247
- Jones, H.D. & Trueman, E.R. (1970). Locomotion of the limpet, *Patella vulgata* L. *Journal of Experimental Biology* 52: 201–216
- Jones, J.B. & Marshall, B.A. (1986). *Cocculinika myzorama* new genus, new species, a parasitic copepod from a deep-sea wood-ingesting limpet. *Journal of Crustacean Biology* 6: 166–169
- Jonges, K. (1980). Genital ducts in several species of the cyclophorid genus *Leptopoma* (Mollusca, Mesogastropoda). *Bijdragen tot de Dierkunde* 50: 292–302
- Jousseume, F.P. (1884). Division des Cypræidae. *Le Naturaliste* 6th year No. 52: 414–415
- Jung, P. (1987). Giant gastropods of the genus *Campanile* from the Caribbean Eocene. *Ecologiae Geologicae Helvetiae* 80: 889–896
- Jung, P. & Abbott, R.T. (1967). The genus *Terebellum* (Gastropoda: Strombidae). *Indo-Pacific Mollusca* 1: 445–454
- Kabat, A.R. (1990a). Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32: 155–193
- Kabat, A.R. (1990b). Species of Naticidae (Mollusca: Gastropoda) described by Linnaeus in the *Systema Naturae* (1758). *Zoological Journal of the Linnean Society* 100: 1–25
- Kaicher, S.D. (1972). A second ovoviviparous *Nassarius*. *The Nautilus* 85: 126–128
- Kantor, Y.I. (1984). Pseudohermaphroditism in *Buccinum undatum* (Gastropoda, Prosobranchia). *Zoologicheskii Zhurnal* 68: 1256–1258
- Kantor, Y.I. (1990a). Anatomical basis for the origin and evolution of the toxoglossan mode of feeding. *Malacologia* 32: 3–18
- Kantor, Y.I. (1990b). *Bryukhonogie mollyuski mirogo okeana: podsemeistvo Volutopsiina*. [Gastropods of the Subfamily Volutopsiinae of the world oceans]. Nauka : Moscow 180 pp.

15. PROSOBRANCHS

- Kantor, Y.I. (1991). On the morphology and relationships of some oliviform gastropods. *Ruthenica* 1: 17–52
- Kantor, Y.I. (1995). On the morphology of the digestive system of *Latiaxis* (*Babelomurex*) (Gastropoda, Coralliophilidae) with notes on the phylogeny of the family. *Ruthenica* 5: 9–15
- Kantor, Y.I. (1996). Phylogeny and relationships of Neogastropoda. Pp. 221–230 in Taylor, J.D. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press: Oxford
- Kantor, Y.I. & Harasewych, M.G. (1992). Morphology of the digestive system of *Volutomitra alaskana* Dall, 1902 (Gastropoda, Pectinibranchia, Volutomitridae), with notes on the possible mechanism of feeding. *Ruthenica* 2(1): 45–53
- Kantor, Y.I. & Medinskaya, A.I. (1991). Morphology and feeding of *Mitrella burchardi* (Gastropoda: Columbellidae). *Asian Marine Biology* 8: 25–33
- Kase, T. (1994). New Species of *Patella* (Gastropoda: Mollusca) from the Miocene and Pliocene of Japan: a clade extinct from the Pacific. *Bulletin of the National Science Museum, Tokyo, Series C* 20: 53–65
- Kase, T. & Hayami, I. (1992). Unique submarine cave mollusc fauna: composition, origin and adaptation. *Journal of Molluscan Studies* 58: 446–449
- Kasinathan, R. (1975). Some studies of five species of cyclophorid snails from peninsular India. *Proceedings of the Malacological Society of London* 4: 379–394
- Kay, E.A. (1960a). The functional morphology of *Cypraea caputserpentis* L. and the interpretation of the relationships among the Cypraeacea. *Internationale Revue Gesamten Hydrobiologie* 45: 175–196
- Kay, E.A. (1960b). Generic revision of the Cypraeinae. *Proceedings of the Malacological Society of London* 33: 278–287
- Kay, E.A. (1963). Anatomical notes on *Cypraea aurantium* Gmelin and other cowries and an examination of the subgenus *Lyncina* Troschel. *Journal of the Malacological Society of Australia* 1(7): 47–61
- Kay, E.A. (1971). The littoral marine molluscs of Fanning Island. *Pacific Science* 25: 260–281
- Kay, E.A. (1979). Hawaiian marine shells. Reef and shore fauna of Hawaii, Section 4: Mollusca. *Bernice P. Bishop Museum Special Publication* No. 64. Bishop Museum Press: Honolulu xviii 653 pp.
- Kay, E.A. (1985). About the cowries. Pp. 4–11 in Burgess, C.M. (ed.) *Cowries of the World*. Gordon Verhoef: Cape Town
- Kay, E.A. (1990). Turrid faunas of Pacific islands. *Malacologia* 32: 79–87
- Kay, E.A., Corpus, G.C. & Magruder, W.H. (1982). *Opihi: Their biology and culture*. Aquaculture Development Program, State of Hawaii, Department of Land and Natural Resources: Honolulu 98 pp.
- Keen, A.M. (1960a). Suborder Patellina von Ihering, 1876. Pp. 1231–1237 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas
- Keen, A.M. (1960b). Vermetid gastropods and marine intertidal zonation. *The Veliger* 3: 1–2
- Keen, A.M. (1961). A proposed reclassification of the gastropod family Vermetidae. *Bulletin of the British Museum (Natural History), Zoology* 7: 183–214
- Keesing, J.K. & Wells, F.E. (1989). Growth of the abalone *Haliotis roei* Gray. *Australian Journal of Marine and Freshwater Research* 40: 199–204
- Kennedy, J.J. (1995). The courtship, pseudo-copulation behaviour and spermatophore of *Turritella communis* Risso 1826 (Prosobranchia: Turritellidae). *Journal of Molluscan Research* 61: 421–434
- Kennedy, J.J. & Keegan, B.F. (1992). The encapsular developmental sequence of the mesogastropod *Turritella communis* (Gastropoda: Turritellidae). *Journal of the Marine Biological Association of the United Kingdom* 72: 783–805
- Keough, M.J., Quinn, G.P. & King, (1993). Correlations between human collecting and intertidal mollusc populations on rocky shores. *Conservation Biology* 7: 378–390
- Kershaw, R.C. (1983). The gastropods *Assimineae* and *Hydrococcus* in Tasmania (Mollusca: Gastropoda). *Records of the Queen Victoria Museum* 83: 1–24
- Kesteven, H.L. (1904). The anatomy of *Megalatractus*. *Australian Museum Memoir* 4: 419–449
- Kiener, L.C. (1838–1839). Vol. 10 *Scalaria*, Cadran (Solarium Lamarck), Rotella, Delphinula. Partie II Genre Cadran (Solium Lamarck). Pp. 1–12 Pl. 1 in Kiener, L.C. (& Fischer, P. partim) (1834–1880) *Spécies Général et Iconographie des Coquilles Vivantes, comprenant la collection du Muséum d'Histoire naturelle de Paris, la collection Lamarck, celle du Prince Masséna ... et les découvertes récentes des voyages*. Paris
- Kiener, L.C. (1841). *Spécies générale et iconographie des coquilles vivantes. Famille des Purpurifères, pt. 2, genre Columbelle*. Balliere: Paris pp. 105–112
- Kilburn, R.N. (1976). A revision of the Naticidae of Southern Africa and Mozambique (Mollusca). *Annals of the Natal Museum* 22: 829–884
- Kilburn, R.N. (1977). Description of new species of *Amalda* and *Chilotygmia* (Gastropoda: Olividae: Ancillinae) with a note on the systematics of *Amalda*, *Ancillus* and *Ancillista*. *Annals of the Natal Museum* 23(1): 13–21
- Kilburn, R.N. (1981). Revision of the genus *Ancilla* Lamarck, 1799 (Mollusca: Olividae: Ancillinae). *Annals of the Natal Museum* 24(2): 349–463
- Kilburn, R.N. (1983–1995). Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique, Parts 1–7. *Annals of the Natal Museum* [part 1 Turrinae, 25: 549–585; part 2, Clavatulininae, 26: 417–440; part 3, Borsoniinae, 27: 633–720; part 4, Drilliinae, Crassispirinae and Strictispirinae, 29: 167–320; part 5, Tarantinae, 32: 325–339; part 6, Mangeliinae, sect. 1, 33: 461–575; part 6, Mangeliinae, sect. 2, 34: 317–367; part 7, Crassispirinae, sect. 2, 35: 177–228; part 8, Mangeliinae, sect. 3, 36: 261–269]
- Kilburn, R.N. (1985). The family Epitoniidae (Mollusca: Gastropoda) in southern Africa and Mozambique. *Annals of the Natal Museum* 27(1): 239–337
- Kilian, E.F. (1951). Untersuchungen zur Biologie von *Pomatias elegans* (Müller) und ihrer 'Konkrementdrüse'. *Archiv für Molluskenkunde* 80: 1–16
- Kilius, R. (1962). Gastropoda/Prosobranchia. Tonnidae. *Das Tierreich* 77: 1–63
- Kilius, R. (1973). Gastropoda/Prosobranchia. Cymatiidae. *Das Tierreich* 92: 1–235
- Kiseleva, G.A. (1967). Influence of the substratum on the settlement and metamorphosis of benthic animals. Pp. 71–84 in Vodnitschii, V.A. (ed.) *Benthic Biocoenoses and Biology of Benthic Animals*. Academy of Sciences of the Ukraine S.S.R.: Kiev [in Russian]
- Kitching, R.L. & Pearson, J. (1981). Prey location by sound in a predatory intertidal gastropod. *Marine Biology Letters* 2: 313–321
- Kitching, R.L. & Zalucki, M.P. (1982). Component analysis and modelling of the movement process: analysis of simple tracks. *Researches in Population Ecology, Kyoto* 24: 224–238
- Kleinsteuber, H. (1913). Die anatomie von *Trochita*, *Calyptraea* and *Janacus*. *Fauna Chilensis* 4: 385–476
- Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. (1960a). Superfamily Patellacea Rafinesque, 1815. Pp. 1231–1236 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas
- Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. (1960b). Systematic descriptions. Pp. 1169–1310 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas

- Knight, J.B., Batten, R.L., Yochelson, E.L. & Cox, L.R. (1960c). Paleozoic and some Mesozoic Caenogastropoda and Opisthobranchia. Pp. 1310–1331 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part 1. Mollusca 1*. Geological Society of America & University of Kansas Press : Boulder, Colorado & Lawrence, Kansas
- Knox, G.A. (1963). The biogeography and intertidal ecology of the Australian coasts. *Oceanography and Marine Biology Annual Review* 1: 341–403
- Knudsen, J. (1950). Egg capsules and development of some marine prosobranchs from tropical West Africa. *Atlantide Report* 1: 85–130
- Knudsen, J. (1991). Observations on *Hipponix australis* (Lamarck, 1819) (Mollusca, Gastropoda, Prosobranchia) from the Albany area, Western Australia. Wells, F.E., Walker, D.I. Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: the Marine Fauna and Flora of Albany, Western Australia* 2: 641–660
- Knudsen, J. (1992). Observations on egg capsules and reproduction of some marine prosobranch molluscs from Hong Kong waters. Pp. 723–744 in Morton, B. (ed.) *The Marine Flora and Fauna of Hong Kong and Southern China III*. Proceedings of the fourth international marine biological workshop: the Marine Flora and Fauna of Hong Kong and southern China, Hong Kong, 11–29 April 1989. Hong Kong University Press : Hong Kong
- Knudsen, J. (1993). Observations on *Antisabia foliacea* Quoy and Gaimard, 1835 (Mollusca, Gastropoda, Prosobranchia) from off Rottnest Island, Western Australia. Pp. 481–495 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Fifth International Marine Biological Workshop: the Marine Flora and Fauna of Rottnest Island, Western Australia. Vol. 1*. Western Australian Museum : Perth
- Kobelt, W. (1897). *Columbella*. Pp. 281–384 in Martini & Chemnitz, *Neues Systematisches Conchylien-Cabinet*. Vol. 3 (1d), Gattung *Columbella*. von Bauer & Raspe : Nurnberg
- Kobelt, W. (1902). Cyclophoridae. *Das Tierreich* 16. Mollusca. Berlin xxxix 662 pp.
- Koch, H.J. (1949). A review of the South African representatives of the genus *Patella* Linnaeus. *Annals of the Natal Museum* 11: 487–517
- Kohn, A.J. (1959). The ecology of *Conus* in Hawaii. *Ecological Monographs* 29: 47–90
- Kohn, A.J. (1961). Studies on spawning behavior, egg masses and larval development in the gastropod genus *Conus*. II. Observations in the Indian Ocean during the Yale Seychelles Expedition. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17: 1–51
- Kohn, A.J. (1968). Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldives and Chagos Islands. *Ecology* 49: 1046–1062
- Kohn, A.J. (1983). Microhabitat factors affecting abundance and diversity of *Conus* on coral reefs. *Oecologia (Heidelberg)* 60: 293–301
- Kohn, A.J. (1985). Evolutionary ecology of *Conus* on Indo-Pacific coral reefs. *Proceedings of the Fifth International Coral Reef Congress* 4: 139–144
- Kohn, A.J. (1992). *A Chronological Taxonomy of Conus, 1758–1840*. Smithsonian Institution Press : Washington 368 pp.
- Kohn, A.J. (1993). Episodic mortality of limpets on a shore platform at Rottnest Island, Western Australia. Pp. 497–508 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Fifth International Marine Biological Workshop: the Marine Flora and Fauna of Rottnest Island, Western Australia. Vol. 2*. Western Australian Museum : Perth
- Kohn, A.J. & Almasi, K.A. (1993). Comparative ecology of a biogeographically heterogeneous *Conus* assemblage. Pp. 523–538 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Fifth International Marine Biological Workshop: the Marine Flora and Fauna of Rottnest Island, Western Australia*. Western Australian Museum : Perth
- Kohn, A.J. & Leviten, P.J. (1976). Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia (Heidelberg)* 25: 190–210
- Kohn, A.J., Myers, E.R. & Meenakshi, V.R. (1979). Interior remodelling of the shell by a gastropod mollusc. *Proceedings of the National Academy of Sciences (U.S.)* 76: 3406–3410
- Kohn, A.J. & Nybakken, J.W. (1975). Ecology of *Conus* on eastern Indian Ocean fringing reefs: diversity of species and resources utilization. *Marine Biology* 29: 211–234
- Kohn, A.J., Nybakken, J.W. & Van Mol, J.-J. (1972). Radula tooth structure of the gastropod *Conus imperialis* elucidated by scanning electron microscopy. *Science, New York* 176(4030): 49–51
- Kohn, A.J. & Perron, F.E. (1994). *Life History and Biogeography: Patterns in Conus*. Oxford University Press : Oxford vii 106 pp.
- Kohn, A.J. & Riggs, A.C. (1975). Morphometry of the *Conus* shell. *Systematic Zoology* 24: 346–359
- Kohnert, R. & Storch, V. (1984). Zur Ultrastruktur der eupyrenen Spermien und Spermio-genese von *Neritina communis* (Quoy and Gaimard) (Mollusca: Gastropoda). *Zoologischer Anzeiger* 212: 85–94
- Kohnert, R. & Storch, V. (1984a). Vergleichend-ultrastrukturelle Untersuchungen zur Morphologie eupyrener Spermien der Monotocardia (Prosobranchia). *Zoologischer Jahrbücher für Anatomie und Ontogenie der Tiere* 111: 51–92
- Kohnert, R. & Storch, V. (1984b). Elektronenmikroskopische Untersuchungen zur Spermio-genese der eupyrenen Spermien der Monotocardia (Prosobranchia). *Zoologischer Jahrbücher für Anatomie und Ontogenie der Tiere* 112: 1–32
- Koike, K. (1985). Comparative ultrastructural studies on the spermatozoa of the Prosobranchia (Mollusca: Gastropoda). *Science Report of the Faculty of Education, Gunma University* 34: 33–153
- Kollmann, H.A. von (1984). *Megalonoda* n.gen. (Melanopsidae, Gastropoda) aus der Oberkeide der Nordlichen Kalkalpen (Osterreich). *Annalen des Naturhistorischen Museums in Wien* 86: 55–62
- Kollmann, H.A. & Yochelson, E.L. (1976). Survey of Paleozoic gastropods possibly belonging to the subclass Opisthobranchia. *Annalen. Naturhistorischen Museums in Wien* 80: 207–220
- Kool, S.P. (1987). Significance of radular characters for reconstruction of thaidid phylogeny (Neogastropoda: Muricacea). *The Nautilus* 101: 117–132
- Kool, S.P. (1993). Phylogenetic analysis of the Rapaninae (Neogastropoda: Muricidae). *Malacologia* 35: 155–259
- Kostitzine, J. (1949). Contribution à l'étude de l'appareil reproducteur femelle de quelques mollusques prosobranches marins. *Archives de Zoologie Expérimentale et Générale* 86: 143–167
- Kosuge, S. (1964). On the systematic position of the family Triphoridae from the viewpoints of their radulae and opercula (A preliminary report). *Venus* 23: 43–47
- Kosuge, S. (1966a). The family Triphoridae and its systematic position. *Malacologia* 4: 297–324
- Kosuge, S. (1966b). Anatomical studies on Japanese Rissoacea (III). On *Truncatella kiusiuensis* Pilsbry. *Science Report of the Yokosuka City Museum* 12: 18–25
- Kosuge, S. (1969). Anatomical study of Japanese Rissoidea (Gastropoda: Prosobranchia). 2. On the family Stenothyridae. *Bulletin of the National Science Museum* 12(2): 217–239
- Kosuge, S. (1986). Description of a new species of ecto-parasitic snail on fish (Gastropoda: Olivacea). *Bulletin of the Institute of Malacology, Tokyo* 2(5): 77–78
- Kosuge, S. & Hayashi, S. (1967). Notes on the feeding habits of *Capulus dilatatus* A. Adams, 1860 (Gastropoda). *Science Reports of the Yokosuka City Museum* 13: 45–54
- Kosuge, S. & Suzuki, M. (1985). Illustrated catalogue of *Latiaxis* and its related groups. Family Coralliophilidae. *Institute of Malacology, Tokyo, Special Publication* 1: 1–83
- Kotaka, T. (1978). World-wide biostratigraphic correlation based on turritellid phylogeny. *The Veliger* 21: 189–196

15. PROSOBRANCHS

- Kretzschmar, C. (1919). Das Nerven-system und osphradiumartige Sinnesorgan der Cyclophoriden. *Fauna et Anatomia Ceylanica*, Nr. 4. *Jenaische Zeitschrift für Naturwissenschaft* 56: 1-84
- Krijgsman, B.J. & Divaris, G.A. (1955). Contractile and pacemaker mechanisms of the heart of molluscs. *Biological Reviews* 30: 1-39
- Krogh, A. (1939). *Osmotic Regulation in Aquatic Animals*. University Press : Cambridge vi 242 pp.
- Kronenberg, G.C. (1994). A review of the Personidae Gray, 1954, with the description of *Distorsio ventricosa* spec. nov. *Vita Marina* 42: 57-103
- Kronenberg, G. & Berkhout, J. (1994). *Strombidae*. Stichting Biologia Maritima : Die Haag
- Kropp, R.K. (1982). Responses of five holothurian species to attacks by a predatory gastropod, *Tonna perdx*. *Pacific Science* 36: 445-452
- Kumar, S.A., Rani, G.A., Leela, A.G.C. & Ayyakkannu, K. (1988). Population structure and sexual dimorphism in the gastropod *Hemifusus pugilinus* (Born). *Indian Journal of Marine Sciences* 17: 240-241
- Kuroda, T. (1962). Notes on the Stenothyridae (aquatic Gastropoda) from Japan and adjacent regions. *Venus* 22(1): 59-69
- Ladd, H.S. (1966). Chitons and gastropods (Haliotidae through Adeorbidae) from the western Pacific Islands. *United States Geological Survey, Professional Paper* 531: 1-98 16 pls
- Ladd, H.S. (1972). Cenozoic fossil mollusks from western Pacific islands; Gastropods (Turritellidae through Strombidae). *United States Geological Survey, Professional Paper* 532: 1-79, 20 pls
- Ladd, H.S. (1977). Cenozoic fossil mollusks from western Pacific islands; Gastropods (Eratoidae through Harpidae). *United States Geological Survey, Professional Paper* 533: iv + 84 pp., pls 1-23
- Lalli, C.M. & Gilmer, R.W. (1989). *Pelagic Snails. The biology of holoplanktonic gastropod molluscs*. Stanford University Press : Stanford xiv 259 pp.
- Lamarck, L.B.P.A. de (1799). Prodrome d'une nouvelle classification des coquilles. *Mémoires de la Société d'Histoire Naturelle de Paris* 1: 63-91
- Lamarck, L.B.P.A. de (1812). *Extrait du cours de zoologie du Muséum d'Histoire Naturelle sur les animaux sans vertèbres; présentant la distribution et les caractères des principales divisions et une simplé liste des genres [Mollusques, Hétero-podes]*. D'Hantel et Gabon : Paris 1-127 pp.
- Lankester, E.R. (1883). *Mollusca*. Pp. 632-695 in *Encyclopedia Britannica*. Vol. 16. London 9th edn
- Largen, M.J. (1971). Genetic and environmental influences upon the expression of shell sculpture in the dog-whelk (*Nucella lapillus*). *Proceedings of the Malacological Society of London* 39: 383-388
- Laseron, C.F. (1950). Review of the Rissoidae of New South Wales. *Records of the Australian Museum* 22: 257-287
- Laseron, C.F. (1951a). Review of the New South Wales Cerithiopsidae. *Australian Zoologist* 11: 351-368
- Laseron, C.F. (1951b). The New South Wales Pyramidellidae and the genus *Mathilda*. *Records of the Australian Museum* 22: 298-334
- Laseron, C.F. (1954a). Revision of the Liotiidae of New South Wales. *Australian Zoologist* 12: 1-25
- Laseron, C.F. (1954b). Revision of the New South Wales Triphoridae. *Records of the Australian Museum* 23: 139-158
- Laseron, C.F. (1954c). *Revision of the New South Wales Turridae*. Australian Zoological Handbook. Royal Zoological Society of New South Wales : Sydney 56 pp.
- Laseron, C.F. (1955). Revision of the New South Wales eulimoid shells. *Australian Zoologist* 12(2): 83-107
- Laseron, C.F. (1956a). The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian zoogeographical provinces. *Australian Journal of Marine and Freshwater Research* 7: 384-484
- Laseron, C.F. (1956b). The family Cerithiopsidae (Mollusca) from the Solanderian and Dampierian zoogeographical provinces. *Australian Journal of Marine and Freshwater Research* 7: 151-182
- Laseron, C.F. (1957). A new classification of the Australian Marginellidae (Mollusca), with a review of species from the Solanderian and Dampierian zoogeographical provinces. *Australian Journal of Marine and Freshwater Research* 8(3): 274-311
- Laseron, C.F. (1958). The family Triphoridae (Mollusca) from northern Australia; also Triphoridae from Christmas Island (Indian Ocean). *Australian Journal of Marine Freshwater Research* 9: 569-658
- Laseron, C.F. (1959). The family Pyramidellidae (Mollusca) from northern Australia. *Australian Journal of Marine and Freshwater Research* 10: 177-267
- Lasiak T. (1990). Asynchronous reproductive activity in the broadcast spawner *Cellana capensis* (Gmelin, 1791) (Gastropoda, Patellidae). *Journal of Molluscan Studies* 56: 69-81
- Lasiak T. (1993). Temporal and spatial variations in exploited and non-exploited populations of the intertidal limpet *Cellana capensis*. *Journal of Molluscan Studies* 59: 295-307
- Lasiak, T.A. & White, D.R.A. (1993). Microalgal food resources and competitive interactions among the intertidal limpets *Cellana capensis* (Gmelin, 1791) and *Siphonaria concinna* Sowerby, 1824. *South African Journal of Marine Science* 13: 97-108
- Laursen, D. (1953). The genus *Ianthina*. *Dana Report* 38: 3-40
- Laursen, D. (1981). Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. *Dana-Report* 89: 1-43
- Lauterbach, K.-E. (1983). Errterungen zur Stammesgeschichte der Mollusca, insbesondere der Conchifera. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 21: 201-216
- Laws, H.M. (1970). Reproductive biology and shell site preferences in *Hipponix conicus* (Schumacher) (Gastropoda: Hipponicidae). *The Veliger* 13: 115-121
- Laxton, J.H. (1969). Reproduction in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). *Zoological Journal of the Linnean Society* 48: 237-253
- Laxton, J.H. (1970a). Shell growth in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 4: 250-260
- Laxton, J.H. (1970b). The relationship between the number of varices and total shell length in some New Zealand Cymatiidae (Gastropoda: Prosobranchia) and its ecological significance. *The Veliger* 13: 127-134
- Laxton, J.H. (1971). Feeding in some Australasian Cymatiidae (Gastropoda: Prosobranchia). *Zoological Journal of the Linnean Society* 50: 1-9
- Leal, J.H. & Bouchet, P. (1989). New deep-water Volutidae from off southeastern Brazil (Mollusca: Gastropoda). *The Nautilus* 103: 1-12
- Lebour, M.V. (1931). The larval stages of *Trivia europaea*. *Journal of the Marine Biological Association of the United Kingdom* 17: 819-832
- Lebour, M.V. (1932). The larval stages of *Sinmia patula*. *Journal of the Marine Biological Society of the United Kingdom* 18: 107-115
- Lebour, M.V. (1933a). The life history of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L.). *Journal of the Marine Biological Association of the United Kingdom* 18: 491-498 477-484
- Lebour, M.V. (1933b). The eggs and larvae of *Turritella communis* Lamarck and *Aporrhais pes-pellicani* (L.). *Journal of the Marine Biological Association of the United Kingdom* 18: 499-506
- Lebour, M.V. (1933c). The British species of *Trivia* : *T. arctica* and *T. monacha*. *Journal of the Marine Biological Association of the United Kingdom* 18: 477-484
- Lebour, M.V. (1933d). The larval stages of *Erato voluta* (Montagu). *Journal of the Marine Biological Association of the United Kingdom* 18: 485-490
- Lebour, M.V. (1934). Rissoid larvae as food of the young herring. The eggs and larvae of the Plymouth Rissoidae. *Journal of the Marine Biological Association of the United Kingdom* 19: 523-539

- Lebour, M.V. (1935). The echinospira larvae of Plymouth. *Proceedings of the Zoological Society of London* 1935: 163–174
- Lebour, M.V. (1937). The eggs and larvae of British prosobranchs with special reference to those living in the plankton. *Journal of the Marine Biological Association of the United Kingdom* 22: 105–166
- Lemche, H. & Wingstrand, K.G. (1959). The anatomy of *Neopilina galathea* Lemche, 1957 (Mollusca, Tryblidiacea). *Galathea Report* 3: 9–71
- Lenderbig, R.E. (1954). Some recent observations on the biology of *Liitorina angulifera* Lam. of Biscayne and Virginia Keys, Florida. *Bulletin of Marine Science* 3: 273–296
- Lester, R.J.G. & Newman, L.J. (1986). First rediae and cercariae to be described from heteropods. *Journal of Parasitology* 72: 195–197
- Levings, S.C. & Garrity, S.D. (1983). Diel and tidal movement of two co-occurring neritid snails: differences in grazing patterns on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* 67: 261–278
- Levinton, J.S. & de Witt, T.H. (1989). Relation of particle-size spectrum and food abundance to particle selectivity in the mud snail *Hydrobia totteni* (Prosobranchia: Hydrobiidae). *Marine Biology* 100: 449–454
- Leviten, P.J. & Kohn, A.J. (1980). Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on intertidal reef rock benches. *Ecological Monographs* 50: 55–75
- Lewis, H. (1972). Notes on the genus *Distorsio* (Cymatiidae) with descriptions of new species. *The Nautilus* 86: 27–50
- Lewis, R., Alewood, P., Dooley, M., Martin, J., Drinkwater, R., Craik, D. & Andrews, P. (1996). Secrets of the cone shell. *Today's Life Science* August 1996: 16–24
- Lilly, M.M. (1953). The mode of life and the structure and functioning of the reproductive ducts of *Bithynia tentaculata* (L). *Proceedings of the Malacological Society of London* 30: 87–110
- Liltved, W.R. (1989). *Cowries and their Relatives of Southern Africa*. Seacomber Publications : Gordon Verhof 208 pp.
- Lindberg, D.R. (1981a). Is there a coiled ancestor in the docoglossan phylogeny? *Annual Report of the Western Society of Malacologists* 13: 15
- Lindberg, D.R. (1981b). Rhodopetalinae, a new subfamily of Acmaeidae from the boreal Pacific: Anatomy and systematics. *Malacologia* 20: 291–305
- Lindberg, D.R. (1981c). *Invertebrates of the San Francisco Bay Estuary System: Mollusca, Family Acmaeidae*. The Boxwood Press : Pacific Grove, California 120 pp.
- Lindberg, D.R. (1982). A multivariate morphometric study of *Notoacmea depicta* (Hinds) and the synonyms *Notoacmea gabatella* (Berry) (Gastropoda: Acmaeidae) and *Notoacmea lepisma* (Berry). *Bulletin of the Southern California Academy of Sciences* 81: 87–95
- Lindberg, D.R. (1983). Anatomy, Systematics, and Evolution of Brooding Acmaeid Limpets. PhD dissertation, Biology, University of California, Santa Cruz
- Lindberg, D.R. (1985). Aplacophorans, monoplacophorans, polyplacophorans and scaphopods: the lesser classes. Pp. 230–247 in Broadhead, T.W. (ed.) *Mollusks. Notes for a Short Course*. University of Tennessee, Department of Geological Science, Studies in Geology Vol. 13
- Lindberg, D.R. (1986a). Radular evolution in the Patellogastropoda. *Bulletin of the American Malacological Union* 4: 115
- Lindberg, D.R. (1986b). Name changes in the 'Acmaeidae'. *The Veliger* 29: 142–148
- Lindberg, D.R. (1988a). The Patellogastropoda. Pp. 35–63 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Lindberg, D.R. (1988b). Heterochrony in gastropods: a neontological view. Pp. 197–216 in McKinney, M. (ed.) *Heterochrony in Evolution: An Interdisciplinary Approach*. Plenum Press : New York
- Lindberg, D.R. (1988c). Recent and Fossil species of the genus *Erginus* from the North Pacific Ocean (Patellogastropoda: Mollusca). *Paleobios* 12: 1–7
- Lindberg, D.R. (1990a). The systematics of *Potamacmaea fluvatilis* Blandford: a brackish water patellogastropod (Patelloidinae: Lottiidae). *Journal of Molluscan Studies* 56: 309–316
- Lindberg, D.R. (1990b). Morphometrics and the systematics of marine plant limpets (Mollusca: Patellogastropoda). Pp. 301–310 in Rohlf, F.J. & Bookstein, F.L. (eds) *Proceedings of the Michigan Morphometrics Workshop, University of Michigan Museum of Zoology Special Publication 2*
- Lindberg, D.R. (1992). Evolution, Distribution and Systematics of Haliotidae. Pp. 3–18 in Shepherd, S.A., Tegner, M.J. & Gutzmán del Prío, S.A. (eds) *Abalone of the World*. Fishing News Books : Oxford, England 608 pp.
- Lindberg, D.R. & Dobberteen, R.A. (1981). Umbilical brood protection and sexual dimorphism in the boreal Pacific trochid gastropod, *Margarites vorticiferus* Dall. *International Journal of Invertebrate Reproduction* 3: 347–355
- Lindberg, D.R. & Dwyer, K.R. (1983). The topography, formation and role of the home depression of *Collisella scabra* (Gould). *The Veliger* 25: 229–237
- Lindberg, D.R. & Hedegaard, C. (1996). A deep water patellogastropod from Oligocene water-logged wood of Washington state, USA (Acmaeidae: Pectinodonta). *Journal of Molluscan Studies* 62: 299–314
- Lindberg, D.R. & Hickman, C.S. (1986). A new anomalous giant limpet from the Oregon Eocene (Mollusca: Patellida). *Journal of Paleontology* 60: 661–668
- Lindberg, D.R. & McLean, J.H. (1981). Tropical eastern Pacific limpets of the family Acmaeidae (Mollusca: Gastropoda): new generic criteria and descriptions of six new species from the mainland and the Galapagos. *Proceedings of the California Academy of Sciences* 42: 323–339
- Lindberg, D.R. & Pearse, J.S. (1990). Experimental manipulations of shell color and morphology of the limpets *Lottia asmi* and *Lottia digitalis* (Mollusca: Patellogastropoda). *Journal of Experimental Marine Biology and Ecology* 140: 173–185
- Lindberg, D.R. & Ponder, W.F. (1996a). An evolutionary tree for the mollusca: Branches or roots? Pp. 67–75 in Taylor, J. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Lindberg, D.R. & Squires, R. (1990). Patellogastropods (Mollusca) from the Eocene Tejon Formation of southern California. *Journal of Paleontology* 64: 578–587
- Lindberg, D.R. & Vermeij, G. (1985). *Patelloida chamorrorum* spec. nov.: a new member of the Tethyan *Patelloida profunda* group (Gastropoda: Acmaeidae). *The Veliger* 27: 411–417
- Lindberg, D.R. & Wright, W.G. (1985). Patterns of sex change of the protandric patellacean limpet *Lottia gigantea* (Mollusca: Gastropoda). *The Veliger* 27: 261–265
- Lindén, O. (1977). Sublethal effects of oil on mollusk species from the Baltic Sea. *Water, Air and Soil Pollution* 8: 305–313
- Linke, O. (1933). Morphologie und Physiologie des Genitalapparatus der Nordsee littorinen. *Wissenschaftliche Meeresuntersuchungen, Abteilung Helgoländer* 19: 1–60
- Linnaeus, C. (1758). *Systema Naturae*, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th edn Holmiae : Laurentii Salvii 2 vols, 1384 pp.
- Linsley, R.M. (1978a). Locomotion rates and shell form in the Gastropoda. *Malacologia* 17: 193–206
- Linsley, R.M. (1978b). Shell form and the evolution of gastropods. *American Scientist* 86: 432–441
- Linsley, R.M. & Javidpour, M. (1980). Episodic growth in Gastropoda. *Malacologia* 20: 153–160
- Linsley, R.M. & Kier, W.M. (1984). The Paragastropoda: a proposal for a new class of Paleozoic Mollusca. *Malacologia* 25: 241–254
- Linsley, R.M. & Yochelson, E.L. (1973). Devonian carrier shells (Euomphalidae) from North America and Germany. *United States Geological Survey, Professional Paper* 824: 1–26

15. PROSOBRANCHS

- Lissmann, H.W. (1945). The mechanism of locomotion in gastropod molluscs. I. Kinematics. *Journal of Experimental Biology* 21: 58–69
- Lissmann, H.W. (1946). The mechanism of locomotion in gastropod molluscs. II. Kinetics. *Journal of Experimental Biology* 22: 37–50
- Little, C. (1965a). Osmotic and ionic regulation in the prosobranch gastropod mollusc *Viviparus viviparus* Linn. *Journal of Experimental Biology* 43: 23–37
- Little, C. (1965b). The formation of urine by the prosobranch gastropod mollusc *Viviparus viviparus* Linn. *Journal of Experimental Biology* 43: 39–54
- Little, C. (1965c). Notes on anatomy of the queen conch, *Strombus gigas*. *Bulletin of Marine Science* 15: 338–358
- Little, C. (1979). Reabsorption of glucose in the renal system of *Viviparus*. *Journal of Molluscan Studies* 45: 207–208
- Little, C. (1981). Osmoregulation and excretion in prosobranch gastropods. Pt 1. Physiology and biochemistry. *Journal of Molluscan Studies* 47: 221–247
- Liu, J.H. (1994a). The ecology of the Hong Kong limpets *Cellana grata* (Gould, 1859) and *Patelloida pygmaea* (Dunker, 1860) – distribution and population dynamics. *Journal of Molluscan Studies* 60: 55–67
- Liu, J.H. (1994b). The ecology of the Hong Kong limpets *Cellana grata* (Gould 1859) and *Patelloida pygmaea* (Dunker 1860), reproductive biology. *Journal of Molluscan Studies* 60: 97–111
- Livshits, G. & Fishelson, L. (1983). Biology and reproduction of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia) in Israel. *Israel Journal of Zoology* 32: 21–35
- Livshits, G., Fishelson, L. & Wise, G.S. (1984). Genetic similarity and diversity of parthenogenetic and bisexual populations of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia). *Biological Journal of the Linnean Society* 23: 41–54
- Loch, I. (1978). Fascioliariidae in North Queensland. *Australian Shell News* No. 22: 4–5
- Loch, I. (1987a). A tremendous *Terebralia*. *Australian Shell News* No. 58: 4
- Loch, I. (1987b). Man bites dog. *Australian Shell News*. 59–60: 9
- Loch, I. (1990). Strombidae in Australia. *Australian Shell News* 71: 5–6
- Loch, I. (1992). *Ataxocerithium*. *Australian Shell News* 78: 1–3
- Loch, I. (1994). *Smaragdia*. *Australian Shell News* 85/86: 1–2
- Long, D.C. (1981). Late Eocene and early Oligocene Turridae (Gastropoda: Prosobranchiata) of the Brown's Creek and Glen Aire Clays, Victoria, Australia. *Memoirs of the National Museum of Victoria* 42: 15–55
- Lopez, G.R. & Kofoed, L.H. (1980). Epipsammic browsing and deposit-feeding in mud snails (Hydrobiidae). *Journal of Marine Research* 38: 585–599
- Lowell, R.B. (1984). Desiccation of intertidal limpets: effects of shell size, fit to substratum, and shape. *Journal of Experimental Marine Biology and Ecology* 77: 197–207
- Lozouet, P. (1985). Compléments à la malacofaune Oligocene (Stampien) de Gaas (Bassin D'Aquitaine, France), 1. Mollusques Saumatres. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 22(3): 125–142
- Lozouet, P. (1986). Les Gastropodes Prosobranches de l'Oligocene Supérieur du Bassin de l'Adour (Systématique, Paléoenvironnements, Paléoclimatologie, Paléobiogéographie). Thesis, Ecole Pratique des Hautes Etudes
- Lozouet, P. (1991). Mollusca Gastropoda: *Eumitra* récentes de la Région néo-calédonienne et *Charitodoron* fossiles de l'Oligocène supérieur d'Aquitaine (Mitridae). *Mémoires of the Muséum National d'Histoire Naturelle, Série A* 150: 205–222
- Lozouet, P. & Maestrati, P. (1982). Nouvelles espèces de mollusques de l'Oligocene (Stampien) pour les bassins de Paris et d'Aquitaine. *Archiv für Molluskenkunde* 112: 165–189
- Ludbrook, N.H. (1941). Gastropoda from the Abattoirs Bore, Adelaide, South Australia, together with a list of some miscellaneous fossils from the bore. *Transactions of the Royal Society of South Australia* 65: 79–102
- Ludbrook, N.H. (1953). Systematic revision of the volutid Genus *Amoria*. *Proceedings of the Malacological Society of London* 30: 131–153
- Ludbrook, N.H. (1956). The molluscan fauna of the Pliocene strata underlying the Adelaide Plains. Part III. Scaphopoda, Polyplacophora, Gastropoda (Haliotidae to Tornidae). *Transactions of the Royal Society of South Australia* 79: 1–36
- Ludbrook, N.H. (1957). The molluscan fauna of the Pliocene strata underlying the Adelaide Plains. IV – Gastropoda (Turritellidae to Struthiolariidae). *Transactions of the Royal Society of South Australia* 80: 17–58, pls I–IV
- Ludbrook, N.H. (1971). Large gastropods of the families Diastomatidae and Cerithiidae (Mollusca: Gastropoda) in southern Australia. *Transactions of the Royal Society of South Australia* 95: 29–48
- Ludbrook, N.H. (1978). Quaternary molluscs of the western part of the Eucla Basin. *Bulletin of the Geological Survey of Western Australia* 125: 1–286
- Ludbrook, N.H. (1980). Non-marine molluscs from dolomitic limestones in the north of South Australia. *Transactions of the Royal Society of South Australia* 104: 83–92
- Ludbrook, N.H. (1983). Molluscan faunas of the Early Pleistocene Point Ellen Formation and Burnham Limestone, South Australia. *Transactions of the Royal Society of South Australia* 107: 37–49
- Ludbrook, N.H. (1984). *Quaternary Molluscs of South Australia*. Department of Mines and Energy, South Australia, Handbook No. 9: 1–327
- Lupu, D. (1979). *Tanzaniella* gen. n. (Gastropoda: Neritidae) from the coast of the Indian Ocean. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa"* 20: 15–19
- Luque, A.A., Templado, J. & Burnay, L.P. (1988). On the systematic position of the genera *Litiopa* Rang, 1829 and *Alaba* H. and A. Adams, 1853. Pp. 180–193 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement* 4
- Lutfy, R.G. & Demian, E.S. (1967). The histology of the alimentary system of *Marisa cornuarietis* (Mesogastropoda: Ampullariidae). *Malacologia* 5: 375–422
- Lützen, J. (1972). Studies on parasitic gastropods from echinoderms. II. On *Stilifer* Broderip, with special reference to the structure of the sexual apparatus and the reproduction. *Biologiske Skrifter. Det Kongelige Danske Videnskabernes Selskab* 19(6): 1–18
- Lützen, J. (1976). On a new genus and two new species of Prosobranchia (Mollusca), parasitic on the tropical sea urchin *Echinometra mathaei*. *Israel Journal of Zoology* 25: 38–51
- Lützen, J. (1979). Studies on the life history of *Enteroxenos Bonnevie*, a gastropod endoparasitic in aspidochirote holothurians. *Ophelia* 18: 1–51
- Lützen, J. & Nielsen, K. (1975). Contributions to the anatomy and biology of *Echineulima* n.g. (Prosobranchia: Eulimidae), parasitic on sea urchins. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 138: 171–199
- Maas, D. (1965). Anatomische und histologische untersuchungen am mundapparat der Pyramidelliden. *Zeitschrift Morphologie und Ökologie der Tiere* 54: 566–642
- MacClintock, C. (1967). Shell structure of patelloid and bellerophonitoid gastropods (Mollusca). *Peabody Museum of Natural History, Yale University, Bulletin* 22: 1–140
- MacDonald, J.D. (1860). Further observations on the metamorphosis of Gasteropoda, and the affinities of certain genera, with an attempted natural distribution of the principal families of the order. *Transactions of the Linnean Society of London* 23: 69–81
- MacDonald, J.D. (1880). On the natural classification of Gastropods. Part 1. *Journal of the Linnean Society of London* 15: 161–167
- MacIntyre, R.J. (1961). Larval development of *Velacumantus australis*. *Proceedings of the Linnean Society of New South Wales* 86: 183–184
- MacKay, D.A. & Underwood, A.J. (1977). Experimental studies on homing in the intertidal patellid limpet *Cellana tramoserica* (Sowerby). *Oecologia (Heidelberg)* 30: 215–237

- Macpherson, J.H. (1955). Preliminary revision of the families Patellidae and Acmaeidae in Australia. *Proceedings of the Royal Society of Victoria* 67: 229–256
- Macpherson, J.H. (1957). A review of the genus *Coxiella* Smith 1894, sensu lato. *Western Australian Naturalist* 5: 191–204
- Macpherson, J.H. & Gabriel, C.J. (1962). *Marine Molluscs of Victoria*. Melbourne University Press and National Museum of Victoria: Melbourne 475 pp.
- Maeda, T. (1986). Interrelationships of types of osphradium, habitat and food habit of the Cerithiacea and its near superfamilies (Mesogastropoda). *Venus* 45: 31–41
- Maes, V.O. (1967). Radulae of two species of *Pleuroploca* (Fascioliariidae) from the Indo-Pacific. *The Nautilus* 81: 48–54
- Maes, V.O. (1971). Evolution of the toxoglossate radula and methods of envenomation. *Annual Report of the American Malacological Union* 1970: 69–72
- Maes, V.O. & Ræihle, D. (1975). Systematics and biology of *Thala floridana* (Gastropoda: Vexillidae). *Malacologia* 15: 43–67
- Mahmoud, I.G. (1956). Etude paléontologiques sur la fauna Crétacique du Massif du Moghara (Sinai-Egypte). *Publications de l'Institut du Désert d'Egypte* 8: 1–195
- Majima, R. (1989). Cenozoic fossil Naticidae (Mollusca: Gastropoda) in Japan. *Bulletin of American Paleontology* 96: 1–159, pls 1–14
- Malek, E.A. & Cheng, T.C. (1974). *Medical and Economic Malacology*. Academic Press: New York x 398 pp.
- Mandahl-Barth, G. (1946). *Diccolax cucumariae*. A new parasitic snail. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 109: 55–68
- Mapstone, B.D., Underwood, A.J. & Creese, R.G. (1984). Experimental analysis of the commensal relation between intertidal gastropods *Patelloida mufria* and the trochid *Austrocochlea constricta*. *Marine Ecology Progress Series* 17: 85–100
- Marche-Marchad, I. (1968). Un nouveau mode de développement intracapulaire chez les mollusques Prosobranches neogastropodes: l'incubation intrapécieuse des *Cymba* (Volutidae). *Compte Rendu de l'Académie des Sciences, Paris* 266: 706–709
- Marcus, Er. & Marcus, Ev. (1962). Studies on Columbelloidea. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia* 24 (261): 335–402
- Marcus, Er. & Marcus, E.deB.R. [Ev.] (1963). Mesogastropoden von der Küste São Paulos. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, Akademie der Wissenschaften und der Literatur, Mainz* 1963 (1): 5–105
- Marcus, E.deB.R. [Ev.] (1987). On *Coriocella nigra* (Blainville, 1824) Gastropoda, Prosobranchia, Lamelliariidae, from the Gulf of Elat. *Israel Journal of Zoology* (1986/87) 34: 1–11
- Marcus, Ev. & Marcus, Er. (1959a). On the reproduction of 'Olivella'. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo* 232: 189–200
- Marcus, Ev. & Marcus, Er. (1959b). Studies on 'Olividae'. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo* 232 Zoologie 22: 99–188, 11 pls.
- Marcus, Ev. & Marcus, Er. (1962). On *Leucozonia nassa*. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo* 261, *Zoologia* 24: 11–30
- Marcus, Ev. & Marcus, Er. (1964a). On *Cerithium atratum* (Born 1778) (Gastropoda: Prosobranchia). *Bulletin of Marine Science of the Gulf and Caribbean* 14: 494–510
- Marcus, Ev. & Marcus, Er. (1964b). On the dove shell, *Anachis pulchella* (Blainv.). *Anais da Academia Brasileira de Ciências* 36: 359–366
- Marcus, Ev. & Marcus, Er. (1965). On Brazilian supratidal and estuarine snails. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia* 287 25: 29–82
- Marcus, Ev. & Marcus, Er. (1967). American opisthobranch mollusks. Part 1. Tropical American opisthobranchs. *Studies in Tropical Oceanography* 6: 3–137
- Marshall, B.A. (1977a). The Recent New Zealand species of *Triforis* (Gastropoda: Triforidae). *New Zealand Journal of Zoology* 4: 101–110
- Marshall, B.A. (1977b). The dextral triforid genus *Metaxia* (Mollusca: Gastropoda) in the south-west Pacific. *New Zealand Journal of Zoology* 4: 111–117
- Marshall, B.A. (1978). Cerithiopsidae (Mollusca: Gastropoda) of New Zealand and a provisional classification of the family. *New Zealand Journal of Zoology* 5: 47–120
- Marshall, B.A. (1979). The Trochidae and Turbinidae of the Kermadec Ridge (Mollusca: Gastropoda). *New Zealand Journal of Zoology* 6: 521–552
- Marshall, B.A. (1980). The systematic position of *Triforis* Deshayes (Mollusca: Gastropoda). *New Zealand Journal of Zoology* 7: 85–88
- Marshall, B.A. (1981). New records of Conidae (Mollusca: Gastropoda) from the New Zealand region. *New Zealand Journal of Zoology* 8: 493–501
- Marshall, B.A. (1983a). The family Cocculinellidae (Mollusca: Gastropoda) in New Zealand. *Records of the National Museum of New Zealand* 2: 139–143
- Marshall, B.A. (1983b). Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand Region. *New Zealand Journal of Zoology* 10: 235–260
- Marshall, B.A. (1983c). A revision of the Recent Triphoridae of southern Australia. *Records of the Australian Museum, Supplement* 2: 1–119
- Marshall, B.A. (1984). Adelacerithiinae: a new subfamily of the Triphoridae (Mollusca: Gastropoda). *Journal of Molluscan Studies* 50: 78–84
- Marshall, B.A. (1985). Recent and Tertiary deep-sea limpets of the genus *Pectinodonta* (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12: 273–282
- Marshall, B.A. (1986). Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12: 505–546
- Marshall, B.A. (1987). Osteopeltidae (Mollusca: Gastropoda): A new family of limpets associated with whale bone in the deep-sea. *Journal of Molluscan Studies* 53: 121–127
- Marshall, B.A. (1988a). Thysanodontinae: a new subfamily of the Trochidae (Gastropoda). *Journal of Molluscan Studies* 54: 215–229
- Marshall, B.A. (1988b). Skeneidae, Vitrinellidae, and Orbistellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History* 22: 949–1004
- Marshall, B.A. (1988c). New Seguenziidae (Mollusca: Gastropoda) from the Tasman, South Pacific, and Southern Antilles Basins. *New Zealand Journal of Zoology* 15: 235–247
- Marshall, B.A. (1991). Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. *Résultats des Campagnes Musorstom. Mémoires du Muséum National d'Histoire Naturelle, Paris (A)* 7: 41–109
- Marshall, B.A. (1992). A revision of the Recent species of *Eudolium* Dall, 1889 (Gastropoda: Tonnoidea). *The Nautilus* 106: 24–38
- Marshall, B.A. (1993). A review of the genus *Kaiparathina* Laws, 1941 (Mollusca: Gastropoda: Trochoidea). *The Veliger* 36: 185–198
- Marshall, B.A. (1994). Deep-sea gastropods from the New Zealand region associated with recent whale bones and an Eocene turtle. *The Nautilus* 108: 1–8
- Marshall, B.A. (1995). Recent and Tertiary Trochaclididae from the Southwest Pacific (Mollusca: Gastropoda: Trochoidea). *The Veliger* 38: 92–115
- Marshall, B.A. (1996). A new subfamily of the Addisoniidae associated with cephalopod beaks from the tropical southwest Pacific, and a new pseudococculinid associated with chondrichthyan egg cases from New Zealand (Mollusca: Lepetelloidea). *The Veliger* 39: 250–259

15. PROSOBRANCHS

- Marshall, D.J. & Hodgson, A.N. (1990). Structure of the cephalic tentacles of some species of prosobranch limpet (Patellidae and Fissurellidae). *Journal of Molluscan Studies* 56: 415–424
- Marshall, P.A. & Keough, M.J. (1994). Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* (Sowerby). *Journal of Experimental Marine Biology and Ecology* 177: 121–138
- Martoja, M. (1975). Le rein de *Pomatias* (=Cyclostoma) elegans (Gastéropode, Prosobranchie): données structurales et analytiques. *Annales des Sciences Naturelles, Zoologie* 17: 535–558
- Marwick, J. (1924). The Struthiolariidae. *Transactions of the New Zealand Institute* 55: 161–190
- Marwick, J. (1950). Notes on the southern family Struthiolariidae. *Journal de Conchyliologie* 90: 234–239
- Marwick, J. (1957). Generic revision of the Turritellidae. *Proceedings of the Malacological Society of London* 32: 144–166
- Marwick, J. (1971). An ovoviviparous gastropod (Turritellidae, Zeacolpus) from the upper Miocene of New Zealand. *New Zealand Journal of Geology and Geophysics* 14: 66–70
- Massin, C. (1982). Contribution to the knowledge of two boring gastropods with an annotated list of the genera *Magilus* Montfort, 1810 and *Leptoconchus* Rüppell, 1835. *Bulletin de l'Institut Royal Sciences Naturelles de Belgique Biologie* 53 (17): 1–28
- Matsukuma, A. (1978). Fossil boreholes made by shell-boring predators or commensals. I. Boreholes of capulid gastropods. *Venus* 37: 29–45
- Matsukuma, A., Okutani, T. & Habe, T. (1991). *World Seashells of Rarity and Beauty*. National Science Museum: Tokyo viii 206 pp.
- Matveeva, T.A. (1955). Biology of *Purpura lapillus* (L.) in the East Murmansk Region. *Biological Studies of the Murmansk Area* 2: 32–47 [in Russian]
- Mawle, E. (1918). Notes on the kelp shell, *Cantharidus irisodontes*. *Australian Zoologist* 1: 161–162
- Maxwell, P.A. (1988). Late Miocene deep-water Mollusca from the Stillwater Mudstone at Greymouth, Westland, New Zealand: paleoecology and systematics. *New Zealand Geological Survey Paleontological Bulletin* 55: 1–120
- Maxwell, P.A. (1992). Eocene Mollusca from the vicinity of McCulloch's Bridge, Waihao River, South Canterbury, New Zealand: paleoecology and systematics. *New Zealand Geological Survey Paleontology Bulletin* 65: 1–280
- May, W.L. (1921). *A Check-list of the Mollusca of Tasmania*. Government Printer: Tasmania 114 pp.
- May, W.L. (1923). *An Illustrated Index of Tasmanian Shells: with 47 plates and 1052 species*. Government Printer: Hobart 99 pp.
- McClatchie, S. (1979). Grazing of *Zeacumantus subcarinatus* on *Ulva lactuca*. *Mauri Ora* 7: 39–45
- McCloskey, L.R. (1973). Development and ecological aspects of the echinospira shell of *Lamellaria rhombica* Dall (Prosobranchia; Mesogastropoda). *Ophelia* 10: 155–168
- McGee, B.L. & Targett, N.M. (1989). Larval habitat selection in *Crepidula* (L.) and its effect on adult distribution patterns. *Journal of Experimental Marine Biology and Ecology* 131: 195–214
- McLean, J.H. (1966). *West American prosobranch gastropods: superfamilies Patellacea, Pleurotomariacea, and Fissurellacea*. PhD thesis, Stanford University, Zoology, California
- McLean, J.H. (1971). A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific. *The Veliger* 14: 114–130
- McLean, J.H. (1984a). A case for derivation of the Fissurellidae from the Bellerophonacea. *Malacologia* 25: 3–20
- McLean, J.H. (1984b). Systematics of *Fissurella* in the Peruvian and Magellanic faunal provinces (Gastropoda: Prosobranchia). *Contributions in Science, Los Angeles* 354: 1–70
- McLean, J.H. (1984c). Shell reduction and loss in fissurellids: a review of genera and species in the Fissurellidae group. *American Malacological Bulletin* 2: 21–34
- McLean, J.H. (1985). The archaeogastropod family Addisoniidae Dall, 1882: life habit and review of species. *The Veliger* 28: 99–108
- McLean, J.H. (1987). Taxonomic description of cocculinid limpets (Mollusca, Archaeogastropoda). Three new species and two rediscovered species. *Zoologica Scripta* 16: 325–333
- McLean, J.H. (1988a). New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea. I. Systematic descriptions. *Philosophical Transactions of the Royal Society of London, Series B* 318: 1–32
- McLean, J.H. (1988b). New archaeogastropod limpet families in the hydrothermal vent community. Pp. 85–87 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- McLean, J.H. (1988c). Three new limpets of the family Pseudococculinidae from abyssal depths (Mollusca, Archaeogastropoda). *Zoologica Scripta* 17: 155–160
- McLean, J.H. (1989a). New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. *Zoologica Scripta* 18: 49–66
- McLean, J.H. (1989b). New Slit limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Pt 1. Systematic descriptions and comparisons based on shell and radula characters. *Contributions in Science, Los Angeles County Museum* 407: 1–29
- McLean, J.H. (1990). Neoleptopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patello-gastropod evolution. *Journal of Zoology, London* 222: 485–528
- McLean, J.H. (1991). Four new pseudococculinid limpets collected by the Alvin in the Eastern Pacific. *The Veliger* 34: 38–47
- McLean, J.H. (1992a). Systematic review of the family Choristellidae (Prosobranchia: Lepetellacea), with descriptions of new species. *The Veliger* 35: 273–294
- McLean, J.H. (1992b). Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. *Journal of Molluscan Studies* 58: 401–414
- McLean, J.H. & Harasewych, M.G. (1995). Revision of the Western Atlantic species of cocculinid and pseudococculinid limpets, with descriptions of new species. *Contributions in Science, Los Angeles County Museum* 453: 1–33
- McLean, J.H. & Haszprunar, G. (1987). Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. *The Veliger* 30: 196–205
- McMahon, R.F. (1985). Interspecific relationships between morphometric parameters and the vertical distribution patterns of seven species of turbanate gastropods on mangrove trees in Hong Kong. Pp. 199–215 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and southern China 2. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 6-24 April 1983*. Hong Kong University Press: Hong Kong
- McMahon, R.F. (1990). Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia* 193: 241–260
- McMahon, R.F. (1991). Upper critical temperature limits, tissue temperatures during emersion and evaporative cooling at elevated temperatures in Western Australian intertidal gastropods: evidence for a physiological barrier at the high tide mark. Pp. 661–673 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: the Marine Flora and Fauna of Albany, Western Australia. Vol. 2*. Western Australian Museum: Perth
- McMahon, R.F. (1992). Microgeographic variation in the shell morphometrics of *Nodilittorina unifasciata* from southwestern Australia in relation to wave exposure off shore. Pp. 107–117 in Grahame, J., Mill, P.J. & Reid, D.G. (eds) *Proceedings of the Third International Symposium on Littorinid Biology*. Malacological Society of London: London
- McMahon, R.F. & Britton, J.C. (1991). The relationship between vertical distribution, rate of evaporative water loss, behaviour during emergence and morphometrics in six species of rocky shore gastropods from Princess Royal Harbour, Western Australia. Pp. 675–692 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *The Marine Flora and Fauna of Albany, Western Australia II*. Western Australian Museum: Perth

- McMichael, D.F. (1959). Marine Mollusca of eastern Australia. 1. The genus *Cymbiolacca* Iredale (Family Volutidae). *Australian Zoologist* 12(4): 374–383
- McMichael, D.F. (1960). Notes on some Australian Volutidae. *Journal of the Malacological Society of Australia* 1(4): 4–13
- McMichael, D.F. (1964). Notes on the genera *Amoria* Gray, 1855, and *Zebromoria* Iredale, 1924, (Gastropoda: Volutidae), with description of new species. *Records of the Australian Museum* 26: 265–274
- McMichael, D.F. (1967). Australian freshwater Mollusca and their probable evolutionary relationships: A summary of present knowledge. Pp. 123–149 in Weatherley, A.H. (ed.) *Australian Inland Waters and their Fauna: Eleven Studies*. Australian National University Press: Canberra
- McMichael, D.F. (1968). Non-marine Mollusca from Tertiary rocks in northern Australia. *Bulletin of the Bureau of Mineral Resources and Geophysics, Australia* 80: 135–157
- McMichael, D.R. & Iredale, T. (1959). The land and freshwater Mollusca of Australia. Pp. 224–245 in Keast, A., Crocker, R.L. & Christian, C.S. (eds) *Biogeography and Ecology in Australia [Monographiae Biologicae 8]*. Junk: Den Haag
- McNair, C.G., Kier, N.M., Lacroix, P.D. & Linsley, R.M. (1981). The functional significance of aperture form in gastropods. *Lethaia* 14: 63–70
- Medem, F.G. von (1945). Untersuchungen über die Ei- und Spermatowirkstoffe bei marinen Mollusken. *Zoologische Jahrbücher, Abteilung Allgemeine Zoologie und Physiologie* 61: 1–44
- Medinskaya, A.I. (1993). Anatomy of the stomach of some Neogastropoda from the offshore zone of the Japan Sea. *Ruthenica* 3(1): 17–24
- Melone, G., Lora Lamia Donin, D. & Cotelli, F. (1980). The paraspermatic cell (atypical spermatozoon) of the Prosobranchia: a comparative ultrastructural study. *Acta Zoologica* 61: 191–201
- Melville, R.V. (1971). The question of the generic name *Vanikoro* Quoy and Gaimard, 1832 (Class Gastropoda) Z.N.(S) 1524. *Bulletin Zoological Nomenclature* 27: 238–245
- Merdsoy, B. & Farley, J. (1973). Phasic activity in the digestive cells of the marine prosobranch gastropod *Littorina littorea* (L.). *Proceedings of the Malacological Society of London* 40: 473–482
- Merrill, A.S. & Boss, K.J. (1964). Reactions of hosts to proboscis penetration by *Odostomia seminuda* (Pyramidellidae). *The Nautilus* 78: 42–45
- Mileikovsky, S.A. (1975). Types of larval development in Littorinidae (Gastropoda: Prosobranchia) of the world ocean, and ecological patterns of their distribution. *Marine Biology* 30: 129–135
- Mill, P.J. & McQuaid, C.D. (eds) (1995). Advances in Littorinid Biology. Proceedings of the Fourth International Symposium on Littorinid Biology, held in Roscoff, France, 19–25 September 1993. *Hydrobiologia* 309: 1–193
- Miller, B.A. (1975). The biology of *Terebra gouldi* Deshayes, 1859, and a discussion of life history similarities among other terebrids of similar proboscis type. *Pacific Science* 29: 227–241
- Miller, B.A. (1979). The biology of *Hastula inconstans* (Hinds, 1844) and a discussion of life history similarities among other hastulas of similar proboscis type. *Pacific Science* 33: 289–306
- Miller, B.A. (1990). The feeding and prey capture mechanism of *Turricula nelliae spurius* (Hedley) (Gastropoda: Turridae). Pp. 979–992 in Morton, B. (ed.) *The Marine Flora and Fauna of Hong Kong and Southern China 2. Volume 3. Behaviour, morphology, physiology and pollution. Proceedings of the Second International Marine Biological Workshop, Hong Kong, 1986*. Hong Kong University Press: Hong Kong
- Miller, J.A. (1989). The toxoglossan proboscis: structure and function. *Journal of Molluscan Studies* 55: 167–181
- Miller, S.L. (1974a). Adaptive design of locomotion and foot form in prosobranch gastropods. *Journal of Experimental Marine Biology and Ecology* 14: 99–156
- Miller, S.L. (1974b). The classification, taxonomic distribution, and evolution of locomotor types among prosobranch gastropods. *Journal of Molluscan Studies* 41: 233–272
- Milne-Edwards, H. (1848). Note sur la classification naturelle chez Mollusques Gastéropodes. *Annales des Sciences Naturelles, Série 3* 9: 102–112
- Minichev, Y.S. & Starobogatov, Y.I. (1979). The subclasses of Gastropoda and their phylogenetic relations. *Zoologicheskii Zhurnal* 58: 293–305
- Moor, B. (1983). Organogenesis. Pp. 123–177 in Wilbur, K.M. (ed.) *The Mollusca. Vol. 3. Development*. Academic Press: New York
- Moore, D.R. (1962). The systematic position of the family Caecidae (Mollusca: Gastropoda). *Bulletin of Marine Sciences of the Gulf and Caribbean* 12(4): 695–701
- Moore, D.R. (1972a). Ecological and systematic notes on Caecidae from St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science* 22(4): 881–899
- Moore, D.R. (1972b). *Cochliolepis parasitica*, a non parasitic marine gastropod, and its place in the Vitrinellidae. *Bulletin of Marine Science* 22(1): 100–112
- Moore, J.E.S. (1898). The molluscs of the great African lakes. II. The anatomy of the *Typhobias*, with a description of the new genus (*Bathanalina*). *Quarterly Journal of Microscopical Science* 41: 181–203
- Moore, J.E.S. (1899). The molluscs of the great African lakes. III. *Tanganyikaia rufofilosa* and the genus *Spekia*. *Quarterly Journal of Microscopical Science* 42: 156–186
- Moran, M.J., Fairweather, P.G. & Underwood, A.J. (1984). Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *Journal of Experimental Marine Biology and Ecology* 75: 1–17
- Moritz, C.E. (1938). The anatomy of the gastropod *Crepidula adunca* Sowerby. *University of California Publications in Zoology* 43: 83–92
- Morrison, J.P.E. (1954). The relationships of old and new world melanians. *Proceedings of the United States National Museum* 103: 357–394
- Morrison, J.P.E. (1965). Notes on the genera of the Hipponicidae. *Annual Report of the American Malacological Union* pp. 33–34
- Morse, E.S. (1910). An early stage of *Acmaea*. *Proceedings of the Boston Society of Natural History* 34: 313–323
- Morton, B. (1985). Prey preference, capture and ration in *Hemifusus tuba* (Gmelin) (Prosobranchia: Melongenidae). *Journal of Experimental Marine Biology and Ecology* 94: 191–210
- Morton, B. (1986a). Reproduction, juvenile growth, consumption and the effects of starvation upon the South China Sea whelk *Hemifusus tuba* (Gmelin) (Prosobranchia: Melongenidae). *Journal of Experimental Marine Biology and Ecology* 102: 257–280
- Morton, B. (1986b). The diet and prey capture mechanism of *Melo melo* (Prosobranchia: Volutidae). *Journal of Molluscan Studies* 52: 156–160
- Morton, B. (1988). *Partnerships in the Sea. Hong Kong's marine symbioses*. Hong Kong University Press: Hong Kong xvi 124pp.
- Morton, B. (1990). Prey capture, preference and consumption by *Linatella caudata* (Gastropoda: Tonnoidea: Ranellidae) in Hong Kong. *Journal of Molluscan Studies* 56: 477–486
- Morton, B. (1991). Aspects of predation by *Tonna zonatum* (Prosobranchia: Tonnoidea) feeding on holothurians in Hong Kong. *Journal of Molluscan Studies* 57: 11–19
- Morton, B. & Morton, J.E. (1983). *The Sea Shore Ecology of Hong Kong*. Hong Kong University Press: Hong Kong xiv 350 pp.
- Morton, J.E. (1950). The Struthiolariidae: Reproduction, life history and relationships. *Transactions and Proceedings of the Royal Society of New Zealand* 78: 451–463
- Morton, J.E. (1951a). The ecology and digestive system of the Struthiolariidae (Gastropoda). *Quarterly Journal of Microscopical Science* 92: 1–25
- Morton, J.E. (1951b). The structure and adaptations of the New Zealand Vermetidae. Part 1. The genus *Serpulorbis*. *Transactions and Proceedings of the Royal Society of New Zealand* 79: 1–19

15. PROSOBRANCHS

- Morton, J.E. (1951c). The structure and adaptations of the New Zealand Vermetidae. Part 2. The genera *Stephopoma* and *Pyxipoma*. *Transactions and Proceedings of the Royal Society of New Zealand* 79: 20–42
- Morton, J.E. (1951d). The structure and adaptations of the New Zealand Vermetidae. Part 3. *Novastoa lamellosa* and its affinities. *Transactions and Proceedings of the Royal Society of New Zealand* 79: 43–51
- Morton, J.E. (1952). A preliminary study of the land operculate *Murdochia pallidum* (Cyclophoridae, Mesogastropoda). *Transactions and Proceedings of the Royal Society of New Zealand* 80: 69–79
- Morton, J.E. (1953a). The functions of the gastropod stomach. *Proceedings of the Linnean Society of London* 164: 240–246
- Morton, J.E. (1953b). *Vermicularia* and the turritellids. *Proceedings of the Malacological Society of London* 30: 80–86
- Morton, J.E. (1955a). The evolution of vermetid gastropods. *Pacific Science* 9: 3–15
- Morton, J.E. (1955b). The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proceedings of the Zoological Society of London* 125: 127–168
- Morton, J.E. (1956). The vascular and nervous systems of *Struthiolaria* (Prosobranchia, Mesogastropoda). *Transactions of the Royal Society of New Zealand, Zoology* 83: 721–743
- Morton, J.E. (1958). The adaptations and relationships of the Xenophoridae (Mesogastropoda). *Proceedings of the Malacological Society of London* 33: 89–101
- Morton, J.E. (1960). The habits of *Cyclope neritea*, a style-bearing stenoglossan gastropod. *Proceedings of the Malacological Society of London* 34: 96–105
- Morton, J.E. (1965). Form and function in the evolution of the Vermetidae. *Bulletin of the British Museum (Natural History), Zoology* 11: 583–630
- Morton, J.E. (1979). *Molluscs*. Hutchison : London 5th edn 264 pp.
- Morton, J.E. & Keen, A.M. (1960). A new species of *Stephopoma* (Siliquariidae: Mesogastropoda) from the eastern Atlantic Ocean. *Proceedings of the Malacological Society of London* 34: 27–35
- Morton, J.E. & Miller, M. (1968). *The New Zealand Sea Shore*. Collins : Auckland 638 pp.
- Morton, J.E. & Yonge, C.M. (1964). Classification and structure of the Mollusca. Pp. 1–58 in Wilbur, K.M. & Yonge, C.M. (eds) *Physiology of the Mollusca. Vol. 1*. Academic Press : New York
- Moses, S.T. (1923). The anatomy of the Chank (*Turbinella pyrum*). *Madras Fisheries Bulletin* 12: 105–107
- Moskalev, L.I. (1970). Gastropod molluscs of the genus *Collisella* (Prosobranchia, Acmaeidae) of the fringing Asian seas of the Pacific Ocean. *Trudy Instituta Okeanologii* 88: 174–212 [in Russian]
- Moskalev, L.I. (1971). New data on the systematic position of the gastropod molluscs of the order Cocculinida Thiele, 1908. Pp. 59–60 in *Molluscs: Ways, methods and results of their investigation* (Autoabstracts of reports of 4th conference on the investigation of molluscs). Academy of Science USSR, Nauka Publishers : Leningrad [in Russian, English translation by G.V. Shkurkin]
- Moskalev, L.I. (1973). Pacific ocean Bathysciadiidae (Gastropoda) and forms similar to them. *Zoologicheskii Zhurnal* 52: 1297–1303 [in Russian, English translation by G.V. Shkurkin]
- Moskalev, L.I. (1976). Concerning the generic diagnosis of the Cocculinidae (Gastropoda, Prosobranchia). *Works of the P.P. Shirshov Institute of Oceanography, Academy of Sciences of the U.S.S.R.* 99: 59–70 [in Russian, English translation by G.V. Shkurkin]
- Moskalev, L.I. (1977). On the revision of mollusks Lepetidae (Gastropoda, Prosobranchia) of the world Ocean. *Works of the P.P. Shirshov Institute of Oceanology, Academy of Sciences U.S.S.R.* 108: 52–78 [in Russian]
- Moskalev, L.I. (1978). Lepetellidae (Gastropoda, Prosobranchia) and forms similar to them. *Works of the P.P. Shirshov Institute of Oceanography, Academy of Sciences of the U.S.S.R.* 113: 132–146 [in Russian, English translation by G.V. Shkurkin]
- Moulton, J.M. (1962). Intertidal clustering of an Australian gastropod. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 123: 170–178
- Moyer, J.T., Emerson, W.K. & Ross, M. (1982). Massive destruction of scleractinian corals by the muricid gastropod, *Drupella*, in Japan and the Philippines. *The Nautilus* 96: 69–82
- Muley, E.V. (1977). Studies on the breeding habits and development of the brood-pouch of a viviparous prosobranch, *Melania scabra*. *Hydrobiologia* 54: 181–185
- Muley, E.V. (1978a). Embryology and development of a freshwater prosobranch, *Melania scabra*. *Hydrobiologia* 58: 89–92
- Muley, E.V. (1978b). Biological and chemical control of the vector snail *Melania scabra* (Gastropoda: Prosobranchia). *Bulletin of the Zoological Survey of India* 1: 1–5
- Murdock, G.R. & Vogel, S. (1978). Hydrodynamic induction of water flow through a keyhole limpet (Gastropoda, Fissurellidae). *Comparative Biochemistry and Physiology* 61A: 227–231
- Murphy, P.G. (1975). *Collisella austrodigitalis* sp. nov.: a sibling species of limpet (Acmaeidae) discovered by electrophoresis. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 155: 193–206
- Murray, F.V. (1959). The animal of *Austroginella johnstoni* (Petterd). *Journal of the Malacological Society of Australia* 1(3): 23–25
- Murray, F.V. (1963). Notes on the spawn and early life history of two species of *Conuber* Finlay & Marwick, 1937 (Naticidae). *Journal of the Malacological Society of Australia* 1(6): 49–58
- Murray, F.V. (1966). A brief account of the spawn of *Conuber incei* (Philippi, 1853) (Gastropoda: Naticidae). *Journal of the Malacological Society of Australia* 1(10): 49–52
- Murray, F.V. (1969). The spawn and early life history of *Cacozeliana granaria* (Kiener 1842) (Gastropoda: Cerithiidae). *Memoirs of the National Museum of Victoria* 29: 111–113
- Murray, F.V. (1970). The reproduction and life history of *Microginella minutissima* (Tenison-Woods, 1876) (Gastropoda: Marginellidae). *Memoirs of the National Museum of Victoria* 31: 31–35
- Murty, A.S. & Rao, M.B. (1978). Effect of environment on the shell shape of a tropical estuarine snail *Neritina violacea* (Gastropoda: Neritacea). *Journal of Molluscan Studies* 44: 265–271
- Nagao, T. (1932). Some Cretaceous Mollusca from Japanese Saghalin and Hokkaido (Lamellibranchiata and Gastropoda). *Journal of the Faculty of Science of Hokkaido University* 4: 23–50
- Nakamura, H.K. (1986). Chromosomes of Archaeogastropoda (Mollusca: Prosobranchia), with some remarks on their cytotaxonomy and phylogeny. *Publications of the Seto Marine Biological Laboratory* 31: 191–267
- Natarajan, A.V. (1954). On the breeding habits of the cowry *Erronea erronea* (Linné). *Current Science, Bangalore* 23: 225–226
- Natarajan, A.V. (1957). Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. *Proceedings of the Indian Academy of Science, Section B* 46: 170–228
- Natarajan, A.V. (1958). Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. *Proceedings of the Indian Academy of Sciences* 46: 170–228
- Neef, G. (1970). Notes on the subgenus *Pellicaria*. *New Zealand Journal of Geology and Geophysics* 13: 436–476
- Newell, R.C. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proceedings of the Zoological Society of London* 144: 25–45
- Newell, R.C. & Kofoed, L.H. (1977). The energetics of suspension-feeding in the gastropod *Crepidula fornicata* L. *Journal of the Marine Biological Association of the United Kingdom* 57: 161–180

- Newell, R.C. & Northcroft, H.R. (1967). A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates. *Journal of Zoology, London* 151: 277–298
- Newell, R.C. & Pye, V.I. (1970a). Seasonal changes in the effect of temperature on the oxygen consumption of the winkle *Littorina littorea* (L.) and the mussel *Mytilus edulis* L. *Comparative Biochemistry and Physiology* 34: 367–383
- Newell, R.C. & Pye, V.I. (1970b). The influence of thermal acclimation on the relation between oxygen consumption and temperature in *Littorina littorea* (L.) and *Mytilus edulis* L. *Comparative Biochemistry and Physiology* 34: 385–397
- Newell, R.C. & Pye, V.I. (1971). Variations in the relationship between oxygen consumption, body size and summated tissue metabolism in the winkle *Littorina littorea*. *Journal of the Marine Biological Association of the United Kingdom* 51: 315–338
- Newman, L.J. (1990a). The taxonomy, biology and distribution of *Atlanta gaudichaudi* Souleyet, 1852 (Gastropoda: Heteropoda) from the waters of the Great Barrier Reef, Australia. *American Malacological Bulletin* 8: 85–94
- Newman, L.J. (1990b). Holoplanktonic molluscs (Gastropoda; Thecosomata, Gymnosomata and Heteropoda) from the waters of Australia and Papua New Guinea: Their Taxonomy, Distribution and Biology. PhD thesis, University of Queensland : Brisbane
- Nicotri, M.E. (1974). Resource partitioning, grazing activities, and influence on the microflora by intertidal limpets. PhD dissertation, Zoology, University of Washington, Seattle, Washington
- Nielsen, C. (1975). Observations on *Buccinum undatum* L. attacking bivalves and on prey responses, with a short review on attack methods of other prosobranchs. *Ophelia* 13: 87–108
- Nielsen, J. & Lethbridge, R. (1989). Feeding and the epiphyte food resources of gastropods living on leaves of the seagrass *Amphibolis griffithii* in south-western Australia. *Journal of the Malacological Society of Australia* 10: 47–58
- Nishihira, M. (1983). Grazing of the mangrove litters by *Terebralia palustris* (Gastropoda: Potamididae) in the Okinawan mangal: preliminary report. *Galaxea* 2: 45–58
- Nishikawa, S. (1962). A comparative study of chromosomes in marine gastropods with some remarks on cytotaxonomy and phylogeny. *Journal of the Shimonoseki College of Fisheries* 11: 149–186
- Nishikawa, S. (1964). Phylogenetical study of the type of the dimorphic spermatozoa in Prosobranchia. *Science Report of the Tokyo Kyoiku Daigaku Section B* 11: 237–275
- Nordsieck, F. (1972). *Die europäischen Meeresschnecken (Opisthobranchia mit Pyramidellidae; Rissoacea) vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer*. Gustav Fischer : Stuttgart 327 pp.
- Nuttall, C.P. & Cooper, J. (1973). A review of some English Palaeogene Nassariidae, formerly referred to *Cominella*. *Bulletin of the British Museum (Natural History), Geology* 23: 179–219
- Nylen, M.U., Provenza, D.V. & Carriker, M.R. (1969). Fine structure of the accessory boring organ of the gastropod, *Urosalpinx*. *American Zoologist* 9: 935–965
- Ökland, S. (1982). The ultrastructure of the heart complex in *Patella vulgata* L. (Archaeogastropoda, Prosobranchia). *Journal of Molluscan Studies* 48: 331–341
- Okutani, T. (1961). Notes on the genus *Carinaria* (Heteropoda) from Japanese and adjacent waters. *Publications of the Seto Marine Biology Laboratory* 9: 333–352
- Okutani, T., Tsuchida, E. & Fujikura, K. (1992). Five bathyal gastropods living within or near *Calypsiogena*-community of the Hatsushima Islet, Sagami Bay. *Venus* 51: 137–148
- Oliver, W.R.B. (1926). Australasian Patelloididae. *Transactions and Proceedings of the New Zealand Institute* 56: 547–582
- Olivera, B.M., Gray, W.R., Zeikus, R., McIntosh, J.M., Varga, J., Rivier, J., de Santos, V. & Cruz, L.J. (1985). Peptide neurotoxins from fish-hunting cone snails. *Science* 230: 1338–1343
- Olivera, B.M., Rivier, J., Clark, C., Ramilo, C.A., Corpuz, G.P., Abogadie, F.C., Mena, E.E., Woodward, S.R., Hillyard, D. & Cruz, L.J. (1990). Diversity of *Conus* neuropeptides. *Science* 249: 257–263
- Olmsted, J.M. (1917). Notes on the locomotion of certain Bermudan mollusks. *Journal of Experimental Zoology, Philadelphia* 24: 223–236
- Olsson, A.A. (1970). The cancellariid radula and its interpretation. *Palaeontographica Americana* 7(43): 19–27
- Olsson, A.A. (1971). Mollusks from the Gulf of Panama, collected by R/V John Elliott Pillsburg, 1967. *Bulletin of Marine Science* 21: 35–92
- Olsson, A.A. & Crovo, L.E. (1968). Observations on aquarium specimens of *Oliva sayana* Ravenel. *The Veliger* 11: 31–32
- Orr, V. (1962). The drilling habit of *Capulus danieli* (Crosse) (Mollusca: Gastropoda). *The Veliger* 5: 63–67
- Orton, J.H. (1909). On the occurrence of protandric hermaphroditism in the mollusc *Crepidula fornicata*. *Proceedings of the Royal Society of London, Series B* 81: 468–484
- Orton, J.H. (1912). The mode of feeding of *Crepidula*, with an account of the current producing mechanism in the mantle cavity, and some remarks on the mode of feeding in gastropods and lamellibranchs. *Journal of the Marine Biological Association of the United Kingdom* 9: 444–478
- Orton, J.H. (1920). Sex-phenomena in the common limpet (*Patella vulgata*). *Nature* 104: 374
- Orton, J.H. (1929). Observations on *Patella vulgata*. Pt III. Habitat and habits. *Journal of the Marine Biological Association of the United Kingdom* 16: 277–288
- Orton, J.H., Southward, A.J. & Dodd, J.M. (1956). Studies on the biology of limpets. Pt II. The breeding of *Patella vulgata* in Britain. *Journal of the Marine Biological Association of the United Kingdom* 35: 149–176
- Osborn, H.L. (1904). Amitosis in the embryo of *Fasciolaria*. *American Naturalist* 38: 869–884
- Ostergaard, J.M. (1950). Spawning and development of some Hawaiian marine gastropods. *Pacific Science* 4: 75–115
- O'Sullivan, J.B., McConnaughey, R.R. & Huber, M.E. (1987). A blood-sucking snail: the Cooper's nutmeg, *Cancellaria cooperi* Gabb, parasitises the California electric ray, *Torpedo californica* Ayres. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 172: 362–366
- Otto, H. & Tönniges, C. (1906). Untersuchungen über die Entwicklung von *Paludina vivipara*. *Zeitschrift für Wissenschaftliche Zoologie, Leipzig* 80: 411–514
- Owen, G. (1966). Digestion. Pp. 53–96 in Wilbur, K.M. & Yonge, C.M. (eds) *Physiology of Mollusca*. Vol. 2. Academic Press : New York
- Owen, G. (1974). Studies on the gill of *Mytilus edulis*: the eulatero-frontal cirri. *Proceedings of the Royal Society of London, Series B* 187: 83–91
- Owre, H.B. (1964). Observations on the development of the heteropod molluscs *Pterotrachea hippocampus* and *Firoloida desmaresti*. *Bulletin of Marine Science of the Gulf and Caribbean* 14: 529–538
- Pace, S. (1902). Contributions to the study of the Columbelloidea. No. 1. *Proceedings of the Malacological Society of London* 5: 36–154
- Pace, S. (1902b). On the identity and relationships of *Buccinum dermestoideum*, Lam.: *Pseudamycla*, nov. gen. *Proceedings of the Malacological Society of London* 5: 253–257
- Pafort-van Iersel, T. (1983). Distribution and variation of Carinariidae and Pterotracheidae (Heteropoda: Gastropoda) of the Amsterdam Mid-North Atlantic Plankton Expedition 1980. *Beaufortia* 33: 73–96
- Paine, R.T. (1966). Function of labial spines, composition of diet, and size of certain marine gastropods. *The Veliger* 9: 17–24
- Palmer, A.R. (1980). Locomotion rates and shell form in the Gastropoda: a re-evaluation. *Malacologia* 19: 289–296
- Palmer, A.R. (1985). Quantum changes in gastropod shell morphology need not reflect speciation. *Evolution* 39: 699–705
- Panetta, P. (1973). *Lepetella laterecompressa* (De Rayneval et Ponzi, 1854). *La Conchiglia* 9: 1–6
- Parker, G.H. (1911). The mechanism of locomotion in gastropods. *Journal of Morphology* 22: 155–170

15. PROSOBRANCHS

- Parkington, J. (1977). Coastal settlement between the mouths of the Berg and Olifants Rivers, Cap Province. *South African Archaeological Bulletin* 31: 127-140
- Parry, G.D. (1978). Effects of growth and temperature acclimation on metabolic rate in the limpet *Cellana tramoserica* (Gastropoda: Patellidae). *Journal of Animal Ecology* 47: 351-368
- Parry, G.D. (1982a). The evolution of the life histories of four species of intertidal limpets. *Ecological Monographs* 52: 65-92
- Parry, G.D. (1982b). Reproductive effort in four species of intertidal limpets. *Marine Biology* 66: 267-282
- Parsons, K.E. & Ward, R.D. (1994). Electrophoretic and morphological examination of *Austrocochlea constricta* (Gastropoda: Trochidae): a species complex. *Australian Journal of Marine and Freshwater Research* 45: 1065-1085
- Patanè, L. (1946a). Sulla biologia di *Littorina punctata* (Gm.). *Bolletino della Società Italiana Biologia Sperimentale* 22: 928-929
- Patanè, L. (1946b). Anaerobiosi in *Littorina neritoides* (L.). *Bolletino della Società Italiana Biologia Sperimentale* 22: 929-930
- Patanè, L. (1955). Cinesi e tropismi, anidro e anaerobiosi in *Littorina neritoides* (L.). (Nota preliminare.) *Bolletino dell'Accademia Scienze Naturale Gioenia Sperimentale* (4) 3: 65-73
- Patil, A.M. (1958). The occurrence of a male of the prosobranch *Potamopyrgus jenkinsi* (Smith) var. *carinata* Marshall in the Thames at Sonning, Berkshire. *Annals and Magazine of Natural History* (13) 1: 232-240
- Patterson, C.M. (1963). Cytological studies of pomatiopsid snails. *Annual Report of the American Malacological Union* 30: 13-14
- Patterson, C.M. (1965). The chromosomes of *Tulotoma angulata* (Streptoneura: Viviparidae). *Malacologia* 2: 259-265
- Pavlichenko, V.I. (1977). The role of *Hydropsyche angustipennis* (Trichoptera: Hydropsychidae) larvae in destroying black flies in flowing reservoirs of the Zaporozhye Oblast, U.S.S.R. *Ekologiya* 1: 104-105
- Pawlik, J.R., O'Sullivan, J.B. & Harasewych, M.G. (1988). The egg capsules, embryos, and larvae of *Cancellaria cooperi* (Gastropoda: Cancellariidae). *The Nautilus* 102: 47-53
- Pearce, J.B. & Thorson, G. (1967). The feeding and reproductive biology of the red whelk *Neptunea antiqua* (L.). (Gastropoda, Prosobranchia). *Ophelia* 4: 277-314
- Pearce, J.B. (1966). On *Lora trevelliiana* (Turton) (Gastropoda: Turridae). *Ophelia* 3: 81-91
- Pechar, P., Prior, C. & Parkinson, B. (1980). *Mitre Shells from the Indian and Pacific Oceans*. Robert Brown & Associates Pty Ltd: Bathurst 126 pp.
- Pechenik, J.A. & Lima, G.M. (1984). Relationship between growth, differentiation, and length of larval life for individually reared larvae of the marine gastropod, *Crepidula fornicata*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 166: 537-549
- Pechenik, J.A., Scheltema, R.S. & Eyster, L.S. (1984). Growth stasis and limited shell calcification in larvae of *Cymatium parthenopeum* during trans-Atlantic transport. *Science* 224: 1097-1099
- Peel, J.S. (1980). A new Silurian retractile monoplacophoran and the origin of the gastropods. *Proceedings of the Geological Association* 91: 91-97
- Pelseneer, P. (1900). Note sur l'organisation du genre *Bathysciadium*. *Bulletin de la Société Zoologique de France* 24: 209-211
- Pelseneer, P. (1911). Recherches sur l'embryologie des Gastropodes. *Mémoires de l'Institut Royal des Sciences Naturelle de Belgique, 2nd Série*, 6: 1-167
- Pelseneer, P. (1926). Notes d'embryologie malacologique. Ponte et développement de *Cypraea europaea*, *Triphoris perversa* et *Lucina lactea*. *Bulletin Scientifique de la France et de la Belgique* 60: 88-112
- Pelseneer, P. (1935). Essai d'Ethologie Zoologique d'après l'étude des mollusques. *Classe des Sciences. Publications Fondation Agathon de Potter*. Académie Royale de Belgique: Bruxelles 662 pp.
- Penchaszadeh, P.E. (1988). Reproductive patterns of some South American Prosobranchia as a contribution to classification. *Malacological Review Supplement* 4: 284-287
- Perrier, R. (1889). Recherches sur l'anatomie et l'histologie du rein des gastéropodes Prosobranchiata. *Annales des Sciences Naturelles, Zoologie* (7) 8: 61-315
- Perron, F.E. (1975). Carnivorous *Calliostoma* (Prosobranchia: Trochidae) from the northeastern Pacific. *The Veliger* 18: 52-54
- Perron, F.E. (1978). The habitat and feeding behavior of the wentletrap *Epitonium greenlandicum*. *Malacologia* 17: 63-72
- Perron, F.E. & Turner, R.D. (1978). The feeding behaviour and diet of *Calliostoma occidentale*, a coelenterate-associated prosobranch gastropod. *Journal of Molluscan Studies* 44: 100-103
- Perry, D.M. (1985). Function of the shell spine in the predaceous rocky intertidal snail *Acanthina spirata* (Prosobranchia: Muricacea). *Marine Biology* 88: 51-58
- Peterson, C.H. & Black, R. (1995). Drilling by buccinid gastropods of the genus *Cominella* in Australia. *The Veliger* 38: 37-42
- Petit, G. & Risbec, J. (1929). Sur la ponte de quelques gastéropodes prosobranches. *Bulletin de la Société Zoologique de France* 54: 564-570
- Petit, R.E. & Harasewych, M.G. (1986). New Philippine Cancellariidae (Gastropoda: Cancellarioidea), with notes on the fine structure and function of the nematoglossan radula. *The Veliger* 28: 436-443
- Petit, R.E. & Harasewych, M.G. (1990). Catalogue of the superfamily Cancellarioidea Forbes and Hanley, 1851 (Gastropoda: Prosobranchia). *The Nautilus, Supplement* 1: 1-69
- Petratits, P.S. (1992). Effects of body size and water temperature on grazing rates of four intertidal gastropods. *Australian Journal of Ecology* 17: 409-414
- Pettitt, C.W. (1974). *An Indexed Bibliography of the Family Littorinidae (Gastropoda: Mollusca) 1758-1973*. Manchester Museum: Manchester 36 pp.
- Petuch, E.J. & Sargent, D.M. (1986). *Atlas of the Living Olive Shells of the World*. Coastal Education and Research Foundation: Fort Lauderdale, Virginia 253 pp.
- Phillips, B.F. (1969). The population ecology of the whelk *Dicathais aegrotata* in Western Australia. *Australian Journal of Marine and Freshwater Research* 20: 225-265
- Phillips, B.F. (1975). Notes on the egg capsules and hatching of *Cronia kavellana* (Reeve, 1846) and the egg capsules *Cronia pseudamygdala* (Hedley, 1903) (Muricidae: Thaidinae). *Journal of Malacological Society of Australia* 3: 59-61
- Phillips, B.F. & Campbell, N.A. (1974). Mortality and longevity in the whelk *Dicathais orbita* (Gmelin). *Australian Journal of Marine and Freshwater Research* 25: 25-33
- Picken, G.B. & Allen, D. (1983). Unique spawning behaviour by the antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). *Journal of Experimental Marine Biology and Ecology* 71: 283-287
- Pilkington, M.C. (1970). Young stages and metamorphosis in an atlantid heteropod occurring off south-eastern New Zealand. *Proceedings of the Malacological Society of London* 39: 117-124
- Pilkington, M.C. (1974). The eggs and hatching stages of some New Zealand prosobranch molluscs. *Journal of the Royal Society of New Zealand* 4: 411-431
- Pilkington, M.C. (1976). Descriptions of veliger larvae of monotocardian gastropods occurring in Otago plankton hauls. *Journal of Molluscan Studies* 42: 337-360
- Pilsbry, H.A. (1891). Acmaeidae, Lepetidae, Patellidae, Titiscaniidae. Parts 49-52 in *Tryon's Manual of Conchology*. Vol. XIII. Philadelphia 195 pp.
- Pilsbry, H.A. (1928). *Georissa*, a land snail genus new to the Hawaiian islands. *Bulletin of the Bernice P. Bishop Museum* 47: 3-4
- Pilsbry, H.A. & Hinkley, A.A. (1909). Melaniidae of the Panuco River system, Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia* 61: 519-531

- Pilsbry, H.A. & Vanatta, E.G. (1904). On certain rachiglossate Gastropoda eliminated from the Aquillidae. *Proceedings of the Academy of Sciences of Philadelphia* 56: 592-595
- Poiner, I.R. & Catterall, C.P. (1988). The effects of traditional gathering on populations of the marine gastropod *Strombus luhuanus* Linne, 1758 in southern Papua New Guinea. *Oecologia (Heidelberg)* 76: 191-199
- Pointier, J.-P. (1989). Conchological studies of *Thiara (Melanoides) tuberculata* (Mollusca: Gastropoda: Thiariidae) in the French West Indies. *Walkerana* 3: 203-209
- Pointier, J.-P., Delay, R., Toffart, J.L., Lefèvre, M. & Romero-Alvarez, R. (1992). Life history traits of three morphs of *Melanoides tuberculata* (Gastropoda: Thiariidae), an invading snail in the French West Indies. *Journal of Molluscan Studies* 58: 415-423
- Pointier, J.-P., Guyard, A. & Mosser, A. (1989). Biological control of *Biomphalaria glabrata* and *B. straminea* by the competitor snail *Thiara tuberculata* in a transmission site of schistosomiasis in Martinique, French West Indies. *Annals of Tropical Medicine and Parasitology* 83: 263-269
- Pointier, J.-P., Théron, A. & Borel, G. (1993). Ecology of the introduced snail *Melanoides tuberculata* (Gastropoda: Thiariidae) in relation to *Biomphalaria glabrata* in the marshy forest zone of Guadeloupe, French West Indies. *Journal of Molluscan Studies* 59: 421-428
- Pointier, J.-P., Toffart, J.L. & Lefèvre, M. (1991). Life tables of freshwater snails of the genus *Biomphalaria* (*B. glabrata*, *B. alexandrina*, *B. straminea*) and of one of its competitors *Melanoides tuberculata* under laboratory conditions. *Malacologia* 33: 43-54
- Ponder, W.F. (1965a). The family Eatoniellidae in New Zealand. *Records of the Auckland Institute and Museum* 6: 47-99
- Ponder, W.F. (1965b). A revision of the New Zealand Recent species previously known as *Notosetia* Iredale, 1915 (Rissoidae, Gastropoda). *Records of the Auckland Institute Museum* 6: 101-130
- Ponder, W.F. (1965c). A revision of the New Zealand Recent and fossil species of *Estea* Iredale, 1915. *Record of the Auckland Institute Museum* 6: 131-161
- Ponder, W.F. (1966a). A new family of the Rissoacea from New Zealand. *Records of the Dominion Museum* 5: 177-184
- Ponder, W.F. (1966b). The New Zealand species previously known as *Zelaxitas* Finlay, 1927 (Mollusca, Gastropoda). *Records of the Dominion Museum, Wellington* 5: 163-176
- Ponder, W.F. (1967). The classification of the Rissoidae and Orbitestellidae with descriptions of some new taxa. *Transactions of the Royal Society of New Zealand, Zoology* 9: 193-224
- Ponder, W.F. (1968a). The morphology of some small New Zealand prosobranchs. *Records of the Dominion Museum* 6: 61-95
- Ponder, W.F. (1968b). Anatomical notes on two species of the Colubrariidae (Mollusca, Prosobranchia). *Transactions of the Royal Society of New Zealand, Zoology* 10: 217-223
- Ponder, W.F. (1968c). Notes on New Zealand prosobranchs with descriptions of new species and subspecies. *Records of the Dominion Museum, Wellington* 6: 113-124
- Ponder, W.F. (1970a). Some aspects of the morphology of four species of the neogastropod family Marginellidae with a discussion on the evolution of the toxoglossan poison gland. *Journal of the Malacological Society of Australia* 2: 55-81
- Ponder, W.F. (1970b). The morphology of *Alciithoe arabica* (Gastropoda: Volutidae). *Malacological Review* 3: 127-165
- Ponder, W.F. (1970c). A new archibenthal species of Fascioliariidae from New Zealand. *Journal of the Malacological Society of Australia* 2: 1-5
- Ponder, W.F. (1971). A review of the New Zealand Recent and fossil species of *Buccinulum* Deshayes (Mollusca: Neogastropoda: Buccinidae). *Journal of the Royal Society of New Zealand* 1: 231-283
- Ponder, W.F. (1972a). The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Neogastropoda). *Malacologia* 11(2): 295-342
- Ponder, W.F. (1972b). Notes on some Australian genera and species of the family Muricidae (Neogastropoda). *Journal of the Malacological Society of Australia* 2: 215-248
- Ponder, W.F. (1972c). Notes on some Australian species and genera of the family Buccinidae (Neogastropoda). *Journal of the Malacological Society of Australia* 2: 249-265
- Ponder, W.F. (1973a). The origin and evolution of Neogastropoda. *Malacologia* 12: 295-338
- Ponder, W.F. (1973b). A review of the Australian species of *Penion* Fischer (Neogastropoda: Buccinidae). *Journal of the Malacological Society of Australia* 2: 401-428
- Ponder, W.F. (1973c). *Pseudoskenella depressa* gen et sp nov., an ectoparasite on *Galeolaria*. *Malacological Review* 6: 119-123
- Ponder, W.F. (1974). A review of the Australian species assigned to *Rissopsis* Garrett with a description of a new species of *Rissopsetia*. *Journal of the Malacological Society of Australia* 3: 25-35
- Ponder, W.F. (1976). Three species of Littorinidae from southern Australia. *Malacological Review* 9: 105-114
- Ponder, W.F. (1980a). Cephalic brood pouches in *Planaxis* and *Fossarus* (Fossaridae and Planaxidae, Cerithiacea, Gastropoda). *Journal of the Malacological Society of Australia* 4: 257-258
- Ponder, W.F. (1980b). The anatomy and relationship of *Hydrococcus brazieri* (T-Woods) (Mollusca: Gastropoda: Rissoacea). *Journal of Molluscan Studies* 48: 64-79
- Ponder, W.F. (1981). *Posticobia norfolkensis* (Sykes), an apparently-extinct, fresh-water snail from Norfolk Island (Gastropoda: Hydrobiidae). *Proceedings of the Linnean Society of New South Wales* 105: 17-21
- Ponder, W.F. (1982). Hydrobiidae of Lord Howe Island (Mollusca: Gastropoda: Prosobranchia). *Australian Journal of Marine and Freshwater Research* 33: 89-159
- Ponder, W.F. (1983a). Review of the genera of the Barleeidae (Mollusca: Gastropoda: Rissoacea). *Records of the Australian Museum* 35: 231-281
- Ponder, W.F. (1983b). Rissoaform gastropods from the Antarctic and sub-Antarctic. The Eatoniellidae, Rissoidae, Barleeidae, Cingulopsidae, Orbitestellidae and Rissoellidae (Mollusca: Gastropoda) of Signy Island, South Orkney Islands, with a review of the Antarctic and sub-Antarctic (excluding southern South America and the New Zealand sub-Antarctic islands) species. *British Antarctic Survey Scientific Reports* 108: 1-96
- Ponder, W.F. (1983c). A revision of the Recent Xenophoridae of the world and of the Australian fossil species (Mollusca, Gastropoda). *Memoirs of the Australian Museum* 17: 1-126
- Ponder, W.F. (1983d). A new species of *Galeodea* (Cassidae, Gastropoda) from Queensland, Australia. *Journal of the Malacological Society of Australia* 6: 91-97
- Ponder, W.F. (1984). A review of the genera of the Iravadiidae (Gastropoda: Rissoacea) with an assessment of the relationships of the family. *Malacologia* 25(1): 21-71
- Ponder, W.F. (1985a). A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Records of the Australian Museum Supplement* 4: 1-221
- Ponder, W.F. (1985b). A revision of the genus *Botelloides* (Mollusca: Gastropoda: Trochacea). *Special Publication of the South Australian Department of Mines and Energy* No. 5: 301-327
- Ponder, W.F. (1985c). The anatomy and relationships of *Emblanda emblematica* (Hedley) (Mollusca: Mesogastropoda: Emblandidae n. fam.). *Records of the Australian Museum* 37: 343-351
- Ponder, W.F. (1985d). The anatomy and relationship of *Elachisina* Dall (Gastropoda: Rissoacea). *Journal of Molluscan Studies* 51: 23-34
- Ponder, W.F. (1986a). Mound springs of the Great Artesian Basin. Pp. 403-420 in De Deckker, P. & Williams, W.D. (eds), *Limnology in Australia. Monographiae Biologiae* 61. CSIRO: Canberra and Dr W. Junk: Dordrecht
- Ponder, W.F. (1986b). Glacidorbidae (Glacidorbacea: Basommatophora), a new family and superfamily of operculate freshwater gastropods. *Journal of the Linnean Society of London* 87: 53-83

15. PROSOBRANCHS

- Ponder, W.F. (1987). The anatomy and relationship of the pyramidellacean limpet *Amathina tricarinata* (Mollusca: Gastropoda). *Asian Marine Biology* 4: 1–34
- Ponder, W.F. (1988a). Bioluminescence in *Hinea braziliana* (Lamarck) (Gastropoda: Planaxidae). *Journal of Molluscan Studies* 54: 361
- Ponder, W.F. (1988b). The truncatelloidean (= rissoacean) radiation – a preliminary phylogeny. Pp. 129–166 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Ponder, W.F. (1988c). *Potamopyrgus antipodarum* – a molluscan coloniser of Europe and Australia. *Journal of Molluscan Studies* 54: 271–285
- Ponder, W.F. (1989a). Mediterranean Cingulopsidae, a relict eastern Tethyan fauna (Gastropoda: Cingulopsoidea). *Bollettino Malacologico Italiano* 25: 85–90
- Ponder, W.F. (1989b). Mollusca. Pp. 71–77 in Zeidler, W. & Ponder, W.F. (eds) *Natural History of Dalhousie Springs*. South Australian Museum : Adelaide
- Ponder, W.F. (1990a). A gravel beach shelled micro-gastropod assemblage from Ceuta, Strait of Gibraltar, with the description of a new truncatelloidean genus. *Bulletin du Muséum National d'Histoire Naturelle Paris, Série 4, Section A Zoology* 12: 291–311
- Ponder, W.F. (1990b). The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). *Journal of Molluscan Studies* 56: 515–532
- Ponder, W.F. (1990c). The anatomy and relationships of a marine valvatoidean (Gastropoda: Heterobranchia). *Journal of Molluscan Studies* 56: 533–555
- Ponder, W.F. (1991a). Marine valvatoideans – implications for early heterobranch phylogeny. *Journal of Molluscan Studies* 57: 21–32
- Ponder, W.F. (1991b). The anatomy of *Diala*, with an assessment of its taxonomic position (Mollusca: Cerithioidea). Pp. 499–519 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: the marine flora and fauna of Albany, Western Australia, Vol. 2*. Western Australian Museum : Perth
- Ponder, W.F. (1991c). The eastern seaboard species of *Jardinella* (Mollusca, Gastropoda, Hydrobiidae), Queensland rainforest-inhabiting freshwater snails derived from the west. *Records of the Australian Museum* 43: 275–289
- Ponder, W.F. (1992a). A new genus and species of aquatic cave-living snail from Tasmania (Mollusca: Gastropoda: Hydrobiidae). *Proceedings of the Royal Society of Tasmania* 126: 23–28
- Ponder, W.F. (1992b). Australian Hydrobiidae – an overview based on current research. Pp. 525–528 in *Proceedings of the Tenth International Malacological Congress, Tübingen 1989*
- Ponder, W.F. (1994a). The anatomy and relationships of *Finella* and *Scaliola* (Caenogastropoda: Cerithioidea: Scaliolidae). Pp. 215–241 in Morton, B. (ed.) *The Malacofauna of Hong Kong and Southern China 3. Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong University Press : Hong Kong
- Ponder, W.F. (1994b). The anatomy and relationships of three species of vitrinelliform gastropods from Hong Kong (Caenogastropoda: Rissoidae). Pp. 243–281 in Morton, B. (ed.) *The Malacofauna of Hong Kong and Southern China 3. Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong University Press : Hong Kong
- Ponder, W.F. (1994c). Australian freshwater Mollusca: conservation priorities and indicator species. *Memoirs of the Queensland Museum* 36: 191–196
- Ponder, W.F. & Clark, G.A. (1988). A morphological and electrophoretic examination of '*Hydrobia buccinoides*', a variable brackish-water gastropod from temperate Australia (Mollusca: Hydrobiidae). *Australian Journal of Zoology* 36: 661–689
- Ponder, W.F. & Clark, G.A. (1990). A radiation of hydrobiid snails in threatened artesian springs in western Queensland. *Records of the Australian Museum* 42: 301–363
- Ponder, W.F., Clark, G.A., Miller, A.C. & Toluzzi, A. (1993). On a major radiation of freshwater snails in Tasmania and eastern Victoria: a preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). *Invertebrate Taxonomy* 7: 501–750
- Ponder, W.F., Colgan, D.J. & Clark, G.A. (1991). The morphology, taxonomy and genetic structure of *Tatea*, estuarine snails from temperate Australia. *Australian Journal of Zoology* 39: 447–497
- Ponder, W.F., Colgan, D.J., Clark, G.A., Miller, A.C. & Terzis, T. (1994). Microgeographic genetic and morphological differentiation of freshwater snails – the Hydrobiidae of Wilsons Promontory, Victoria, south-eastern Australia. *Australian Journal of Zoology* 42: 557–678
- Ponder, W.F., Colgan, D.J., Terzis, T., Clark, S.A. & Miller, A.C. (1996). Three new morphologically and genetically determined species of hydrobiid gastropods from Dalhousie Springs, northern South Australia, with the description of a new genus. *Molluscan Research* 17: 49–109
- Ponder, W.F. & Creese, R.G. (1980). A revision of the Australian species of *Notoacmea*, *Collisella* and *Patelloida* (Mollusca: Gastropoda: Acmaeidae). *Journal of the Malacological Society of Australia* 4: 167–208
- Ponder, W.F. & Darragh, T.A. (1975). The genus *Zemira* H. and A. Adams (Mollusca: Neogastropoda). *Journal of the Malacological Society of Australia* 3: 89–105
- Ponder, W.F. & de Keyser, R. (1992). A revision of the genus *Diala* (Gastropoda: Cerithioidea: Dialidae). *Invertebrate Taxonomy* 6: 1019–1075
- Ponder, W.F., Egger, P. & Colgan, D.J. (1995). Genetic differentiation of aquatic snails (Gastropoda: Hydrobiidae) from artesian springs in arid Australia. *Biological Journal of the Linnean Society* 56: 553–596
- Ponder, W.F. & Gooding, R.U. (1978). Four new eulimid gastropods associated with shallow-water diadematid echinoids in the western Pacific. *Pacific Science* 32: 157–181
- Ponder, W.F. & Hall, S.J. (1983). Pelyciidiidae, a new family of archaeogastropod mollusks. *The Nautilus* 97: 30–35
- Ponder, W.F., Hershler, R. & Jenkins, B.J. (1989). An endemic radiation of hydrobiid snails from artesian springs in northern South Australia: their taxonomy, physiology, distribution and anatomy. *Malacologia* 31: 1–140
- Ponder, W.F. & Lindberg, D.R. (1996). Gastropod phylogeny – challenges for the 90's. Pp. 135–154 in Taylor, J.D. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Ponder, W.F. & Lindberg, D.R. (1997). Towards a phylogeny of gastropod molluscs – an analysis using morphological characters. *Zoological Journal of the Linnean Society* 19(2): 83–265
- Ponder, W.F. & Rosewater, J. (1979). Rectifications in the nomenclature of some Indo-Pacific Littorinidae. *Proceedings of the Biological Society of Washington* 92: 773–782
- Ponder, W.F. & Taylor, J.D. (1992). Predatory shell drilling by two species of *Austroginella* (Gastropoda: Marginellidae). *Journal of Zoology, London* 228: 317–328
- Ponder, W.F. & Vokes, E.H. (1988). A revision of the Indo-West Pacific fossil and Recent species of *Murex* s.s. and *Haustellum* (Mollusca: Gastropoda: Muricidae). *Records of the Australian Museum Supplement* 8: 1–157
- Ponder, W.F. & Warén, A. (1988). Appendix. Classification of the Caenogastropoda and Heterostropho – a list of the family-group names and higher taxa. Pp. 288–328 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Ponder, W.F. & Worsfold, T.M. (1994). A review of the rissoiform gastropods of south-western South America (Mollusca, Gastropoda). *Contributions in Science (Los Angeles)* 445: 1–63
- Ponder, W.F. & Yoo, E.K. (1976). A revision of the Australian and tropical Indo-Pacific Tertiary and Recent species of *Pisinnia* (= *Estea*) (Mollusca: Gastropoda: Rissoidae). *Records of the Australian Museum* 30: 150–247

- Ponder, W.F. & Yoo, E.K. (1977). A revision of the Australian species of the Rissoellidae (Mollusca: Gastropoda). *Records of the Australian Museum* 31: 133–185
- Ponder, W.F. & Yoo, E.K. (1978). A revision of the Eatoniellidae of Australia (Mollusca: Gastropoda: Littorinacea). *Records of the Australian Museum* 31: 606–658
- Ponder, W.F. & Yoo, E.K. (1980). A review of the genera of the Cingulopsidae with a revision of the Australian and tropical Indo-Pacific species (Mollusca: Gastropoda: Prosobranchia). *Records of the Australian Museum* 33: 1–88
- Pope, E.C. (1955). Bather's itch, or schistosome dermatitis. *Australian Museum Magazine* 11: 288–291
- Poppe, G.T. & Goto, Y. (1992). *Volutes*. Mostra Mondiale Malacologia : Italy 348 pp.
- Portmann, A. (1930). Die Larvalnieren von *Buccinum undatum* L. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 10: 410–410
- Povey, A. & Keough, M.J. (1991). Effects of trampling on plant and animal populations on rocky shores. *Oikos* 61: 355–368
- Powell, A.W.B. (1942). The New Zealand Recent and fossil Mollusca of the family Turridae with general notes on turrid nomenclature and systematics. *Bulletin of the Auckland Institute and Museum* No. 2 188 pp.
- Powell, A.W.B. (1944). The Australian Tertiary Mollusca of the family Turridae. *Records of the Auckland Institute and Museum* 3(1): 1–68
- Powell, A.W.B. (1951). Antarctic and Subantarctic Mollusca. Pelecypoda and Gastropoda. *Discovery Reports* 26: 47–196
- Powell, A.W.B. (1964). The Family Turridae in the Indo-Pacific. Part 1. The subfamily Turrinae. *Indo-Pacific Mollusca* 1: 227–346
- Powell, A.W.B. (1966). The molluscan families Speightiidae and Turridae. *Bulletin of the Auckland Institute and Museum* 5: 1–192
- Powell, A.W.B. (1969). The Family Turridae in the Indo-Pacific. Pt. 2. *Indo-Pacific Mollusca* 2: 215–415
- Powell, A.W.B. (1973). The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca* 3(15): 75–206
- Powell, A.W.B. (1979). *New Zealand Mollusca. Marine, Land and Freshwater Shells*. Collins : Auckland xiv 500 pp.
- Prashad, B. (1928). Recent and fossil Viviparidae. A study in distribution, evolution and palaeogeography. *Memoirs of the Indian Museum* 8: 153–251
- Prashad, B. (1932). *Pila* (the apple snail). *Indian Zoological Memoirs* 4: 1–83
- Prince, J.D. & Shepherd, S.A. (1992). Australian abalone fisheries and their management. Pp. 407–426 in Shepherd, S.A., Tegner, M.J. & Guzmán del Prío, S.A. (eds) *Abalone of the World*. Fishing News Books : Oxford, England
- Purchon, R.D. (1968). *The Biology of the Mollusca*. Pergamon Press : London xxv 560 pp.
- Quinn, J.F. (1980). A new genus, species and subspecies of Oocorythidae (Gastropoda: Tonnacea) from the Western Atlantic. *The Nautilus* 94: 149–158
- Quinn, J.F. Jr (1983a). A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). 1. Summary and evaluation of the superfamily. *Proceedings of the Biological Society of Washington* 96: 725–757
- Quinn, J.F. Jr (1983b). *Carenzia*, a new genus of Seguenziaceae (Gastropoda: Prosobranchia) with the description of a new species. *Proceedings of the Biological Society of Washington* 96: 355–364
- Quinn, J.F. Jr (1987). A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). 2. The new genera *Hadroconus*, *Rotellenzia*, and *Asthelys*. *The Nautilus* 101: 59–68
- Quinn, J.F. (1989). Pleioptygmatidae, a new family of mitriform gastropods (Prosobranchia: Neogastropoda). *The Nautilus* 103: 13–19
- Quinn, J.F. Jr (1991). Systematic position of *Basilissopsis* and *Guttula*, and a discussion of the phylogeny of the Seguenzioidae (Gastropoda: Prosobranchia). *Bulletin of Marine Science* 49: 575–598
- Quoy, J.R.C. & Gaimard, J.P. (1830–1834). *Voyages de découvertes de l'Astrolabe exécuté par ordre du Roi pendant les années 1826–1827–1828–1829 sous le commandement de M.J. Dumont d'Urville*. Zoologie. J. Tastu : Paris, 4 vols, 1 268 pp., 686 pp., 945 pp., 390 pp., atlas 198 pp.
- Radoman, P. (1973). New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. *Posebna Izdanja. Prirodnjacki Musej u Beogradu* 32: 1–30.
- Radoman, P. (1983). *Hydrobioidea a superfamily of Prosobranchia (Gastropoda). I. Systematics*. Serbian Academy of Sciences and Arts : Belgrade 256 pp.
- Radwin, G.E. (1977). The family Columbelloidea in the Western Atlantic. *The Veliger* 19: 403–417
- Radwin, G.E. (1978). The Family Columbelloidea in the Western Atlantic. Part 26 - the Pyreninae (continued). *The Veliger* 20(4): 328–344
- Radwin, G.E. & D'Attilio, A. (1976). *Murex Shells of the World. An illustrated guide to the Muricidae*. Stanford University Press : Stanford, California 284 pp.
- Raeihle, D. (1970). Egg cases of *Nitidella ocellata* Gmelin and an *Anachis*. *Annual Report of the American Malacological Union, Pacific Division*, 1969 35: 25–26
- Raffaelli, D.G. (1982). Recent ecological research on some European species of *Littorina*. *Journal of Molluscan Studies* 48: 342–354
- Ragozzi, A. (1985). A proposito di *Addisonia lateralis*. *Notizario C.I.S.M.A.* 6: 53
- Rainer, S.F. (1982). Trophic structure and production in the macrobenthos of a temperate Australian estuary. *Estuarine, Coastal and Shelf Science* 15: 423–441
- Ralph, P.M. (1957). A guide to the New Zealand heteropod molluscs. *Tuatara*, Wellington 6: 116–120
- Ramamoorthi, K. (1955). Studies in the embryology and development of some melaniid snails. *Journal of the Zoological Society of India* 7: 25–34
- Ramamoorthi, K. & Natarajan, R. (1973). Spawning in *Telescopium telescopium* (Linnaeus) (Potamidae, Gastropoda). *Venus* 31: 158–159
- Rambabu, A.V.S. & Rao, M.B. (1992) The resistance of a tropical mud snail, *Telescopium telescopium* (L.) to high temperatures, salinity and desiccation. Pp. 275–281 in Gittenberger, E. & Goud, J. (eds) *Proceedings of the Ninth International Malacological Congress, Edinburgh*. Unitas Malacologica and the National Museum of Natural History, Netherlands : Leiden
- Rammelmeyer, H. (1925). Zur morphologie der *Puncturella noachina*. *Zoologischer Anzeiger* 64: 105–114
- Ramsay, J.A. (1952). *A Physiological Approach to the Lower Animals*. University Press : Cambridge ix 148 pp.
- Randall, J.E. (1964). Contributions to the biology of the queen conch *Strombus gigas*. *Bulletin of Marine Science* 14: 246–295.
- Randles, W.B. (1900). On the anatomy of *Turritella communis*, Risso. *Proceedings of the Malacological Society of London* 4: 56–65
- Ranson, G. (1967). Les Protoconques ou coquilles larvaires des cyprières. *Mémoires, Muséum National d'Histoire Naturelle, Série A Zoologie* 47: 93–126
- Rao, M.B. & Ramasarma, D.V. (1980). Spawning and larval development of *Clypeomorus clypeomorus* Jousseaume 1888 in Waltair coast. *Journal of Molluscan Studies* 46: 186–191
- Rao, M.B. & Sukumar, R.V. (1982). Distribution, zonation and habits of a tropical mud snail *Cerithidea cingulata* (Gmelin) (Mollusca: Gastropoda). *Malacologia* 22: 553–558
- Rath, E. (1988). Organization and systematic position of the Valvatidae. Pp. 194–204 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Raven, C.P. (1966). *Morphogenesis. The analysis of molluscan development*. Oxford University Press : Oxford 2nd edn xii 311 pp.
- Récluz, C.A. (1945). Monographie du genre *Narica*. *Magazin de Zoologie* 7–8: 1–64, pls 117–135
- Rees, W.J. (1964). A review of breathing devices in land operculate snails. *Proceedings of the Malacological Society of London* 36: 55–67

15. PROSOBRANCHS

- Rehder, H.A. (1973). The family Harpidae of the world. *Indo-Pacific Mollusca* 3(16): 207–274
- Rehder, H.A. & Wilson, R.R. (1975). New species of marine molluscs from Pitcairn Island and the Marquesas. *Smithsonian Contributions to Zoology* No. 203: 1–16
- Rehfeldt, N. (1968). Reproductive and morphological variations in the prosobranch '*Rissoa membranacea*'. *Ophelia* 5: 157–173
- Reichelt, R.E. & Kohn, A.J. (1985). Feeding and distribution of predatory gastropods on some Great Barrier Reef platforms. *Proceedings of the Fifth International Coral Reef Congress* 5: 191–196
- Reid, D.G. (1985). Habitat and zonation patterns of *Littoraria* species (Gastropoda: Littorinidae) in Indo-Pacific mangrove forests. *Biological Journal of the Linnean Society* 26: 39–68
- Reid, D.G. (1986a). *Mainwaringia* Nevill, 1885, a littorinid genus from Asiatic mangrove forests, and a case of protandrous hermaphroditism. *Journal of Molluscan Studies* 52: 225–242
- Reid, D.G. (1986b). *The Littorinid Molluscs of Mangrove Forests in the Indo-Pacific Region: the genus Littoraria* (Mollusca: Gastropoda: Littorinidae). British Museum (Natural History): London xv 228 pp.
- Reid, D.G. (1987). Natural selection for apostasy and crypsis acting on the shell colour polymorphism of a mangrove snail, *Littoraria filosa* (Sowerby) (Gastropoda: Littorinidae). *Biological Journal of the Linnean Society* 30: 1–24
- Reid, D.G. (1988). The genera *Bembicium* and *Risellopsis* (Gastropoda: Littorinidae) in Australia and New Zealand. *Records of the Australian Museum* 40: 91–150
- Reid, D.G. (1989a). The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London, Series B* 324: 1–110
- Reid, D.G. (1989b). Systematic revision of the Recent species of *Peasiella* (Gastropoda, Littorinidae), with notes on the fossil species. *Nautilus* 103: 43–69
- Reid, D.G. (1992a). The gastropod family Littorinidae in Hong Kong. Pp. 187–210 in Morton, B. (ed.) *The marine flora and fauna of Hong Kong and southern China III. Vol. 1. Introduction, taxonomy and ecology. Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11–29 April 1989. Hong Kong University Press: Hong Kong.*
- Reid, D.G. (1992b). The evolution of spawn and larval development in the Littorinidae (Gastropoda, Prosobranchia). Pp. 515–516 in *Proceedings of the Tenth International Malacological Congress, Tübingen, 1989*
- Reid, D.G. (1992c). Predation by crabs on *Littoraria* species (Littorinidae) in a Queensland mangrove forest. Pp. 141–151 in Grahame, J., Mill, P.J. & Reid, D.G. (eds) *Proceedings of the Third International Symposium on Littorinid Biology. Malacological Society of London: London*
- Reid, D.G. (1996) *Systematics and Evolution of Littorina*. Ray Society: London 463 pp.
- Renaud, L. (1976). Observations on the behaviour and shell types of *Cypraea moneta* (Mollusca, Gastropoda) at Eniwetok, Marshall Islands. *Pacific Science* 30: 147–158
- Retzius, G. (1906). Die Spermeien der Gasteropoden. *Biologische Untersuchungen* 13: 1–36
- Reynell, A. (1905). Some account of the anatomy of *Cassidaria rugosa* (Linn.). *Proceedings of the Malacological Society of London* 6: 292–299
- Reynolds, W.W. & Reynolds, L.J. (1977). Zoogeography and the predator-prey 'arms race': a comparison of *Eriphia* spp. and *Nerita* spp. from three faunal regions. *Hydrobiologia* 56: 63–67
- Richter, G. (1961). Die Radula der Atlantiden (Heteropoda: Prosobranchia) und ihre Bedeutung für die Systematik und Evolution der Familie. *Zeitschrift für Morphologie und Ökologie der Tiere* 50: 163–238
- Richter, G. (1968). Heteropoden und heteropodenlarven im Oberflächenplankton des Golfs von Neapel. *Pubblicazioni della Stazione Zoologica di Napoli* 36: 346–400
- Richter, G. (1974). Die Heteropoden der "Meteor" Expedition in den Indischen Ozean 1964/65. *Meteor Forschung-Ergebnisse, Reihe D* 17: 55–78
- Richter, G. (1982). Mageninhaltsuntersuchungen an *Oxygyrus keraudreni* (Lesueur) (Atlantidae: Heteropoda). Beispiel einer Nahrungskette im tropischen Pelagial. *Senckenbergiana Maritima* 14: 44–77
- Richter, G. (1984). Die Gehäuseentwicklung bei den Larven der Cymatiiden (Prosobranchia: Tonnacea). *Archiv für Molluskenkunde* 15: 125–141
- Richter, G. (1986). Zur Kenntnis der Gattung *Atlanta* II. *Atlanta lesueuri* Souleyet und *Atlanta oligogyra* Tesch. *Archiv für Molluskenkunde* 117: 19–31
- Richter, G. (1987). Zur Kenntnis der Gattung *Atlanta* III. *Atlanta inflata*, *A. helicinoides*, *A. echinogyra* und *A. plana* (Prosobranchia: Heteropoda). *Archiv für Molluskenkunde* 117: 177–201
- Richter, G. (1989). Zur Kenntnis der Gattung *Atlanta* (IV). Die *Atlanta inclinata*-Gruppe (Prosobranchia: Heteropoda). *Archiv für Molluskenkunde* 119: 259–275
- Riedel, F. (1992). A re-evaluation of the ontogeny of *Cabestana spengleri* (Perry, 1811) (Gastropoda: Tonnoidea: Ranellidae). *The Veliger* 35: 117–121
- Riedel, F. (1994). Recognition of the superfamily Ficoidea Meek 1864 and definition of the Thalassocynidae fam. nov. (Gastropoda). *Zoologische Jahrbücher Abteilung für Systematik* 121: 457–474
- Riedel, F. (1995). An outline of cassoidean phylogeny (Mollusca, Gastropoda). *Contributions to Tertiary and Quaternary Geology* 32(4): 97–132
- Riese, K. (1931). Phylogenetische Betrachtungen über das Nervensystem von *Cypraea moneta* auf Grund seiner Morphologie und Histologie. *Jenaische Zeitschrift für Naturwissenschaften* 65: 361–486
- Risbec, J. (1927). De l'anatomie de trois strombidés et du *Modulus candidus*, Petit qu'on trouve vivant sur la côte de la presqu'île de Nouméa. *Annales du Musée d'Histoire Naturelle de Marseille* 21: 1–18, pl. 28
- Risbec, J. (1928). Contribution à l'étude anatomique de quelques espèces de Mitres de la presqu'île de Nouméa. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 34: 105–112, 173–180, 225–227
- Risbec, J. (1931). Notes sur la reproduction de quelques Prosobranches Néo-calédoniens. *Annales de l'institut Océanographique, Monaco* 10: 23–33
- Risbec, J. (1935). Biologie et ponte de Mollusques Gastéropodes Néo-Calédoniens. *Bulletin de la Société Zoologique de France* 60: 387–417
- Risbec, J. (1937). Anatomie des Cypraeidae. *Archives du Muséum d'Histoire Naturelle, Paris* 14: 75–104
- Risbec, J. (1942). Recherches anatomiques sur les Prosobranches de Nouvelle-Calédonie. (Troisième partie) (1). *Annales des Sciences Naturelles, Zoologie 11^e série*, 4: 21–84
- Risbec, J. (1954). Sur l'anatomie des Columbelles (Gastéropodes Prosobranches). *Bulletin de la Société Zoologique de France* 79: 127–134
- Risbec, J. (1955). Considérations sur l'anatomie comparée de la classification des gastéropodes prosobranches. *Journal de Conchyliologie* 95: 45–82
- Robertson, R. (1958). The family Phasianellidae in the western Atlantic. *Johnsonia* 3: 245–283
- Robertson, R. (1959). Observations on the spawn and veligers of conchs (*Strombus*) in the Bahamas. *Proceedings of the Malacological Society of London* 33: 164–170
- Robertson, R. (1961a). The feeding of *Strombus* and related herbivorous marine gastropods: with a review of field observations. *Notulae Naturae* 343: 1–9
- Robertson, R. (1961b). A second Western Atlantic *Rissoella* and a list of the species in the Rissoellidae. *The Nautilus* 74: 131–136; 75: 21–26
- Robertson, R. (1962). *Vanikoro* Quoy and Gaimard, 1832 (Mollusca, Gastropoda); proposed validation under the plenary powers. Z.N.(S) 1524. *Bulletin of Zoological Nomenclature* 19: 332–336

- Robertson, R. (1963a). The hyperstrophic larval shells of the Architectonicidae. *Annual Report of the American Malacological Union* 1963: 11–12
- Robertson, R. (1963b). Wentletraps (Epitoniidae) feeding on sea anemones and corals. *Proceedings of the Malacological Society of London* 35: 51–63
- Robertson, R. (1964). Dispersal and wastage of larval *Philippia krebsii* (Gastropoda: Architectonicidae) in the North Atlantic. *Proceedings of the Academy of Natural Sciences of Philadelphia* 116: 1–27
- Robertson, R. (1967). *Heliacus* (Gastropoda: Architectonicidae) symbiotic with Zoanthinaria (Coelenterata). *Science* 156: 246–248
- Robertson, R. (1970a). Systematics of Indo-Pacific *Philippia* (*Psilaxis*), architectonicid gastropods with eggs and young in the umbilicus. *Pacific Science* 24: 66–83
- Robertson, R. (1970b). Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. *Pacific Science* 24: 43–54
- Robertson, R. (1971a). Sexually dimorphic archaeogastropods and radulae. *Annual Report of the American Malacological Union* 1970: 75–78
- Robertson, R. (1971b). Scanning electron microscopy of planktonic larval marine gastropod shells. *The Veliger* 14: 1–12
- Robertson, R. (1973a). The biology of the Architectonicidae, gastropods combining prosobranch and opisthobranch traits. *Malacologia* 14: 215–220
- Robertson, R. (1973b). The genus *Gabrielona* (Phasianellidae) in the Indo-Pacific and West Indies. *Indo-Pacific Mollusca* 3: 41–61
- Robertson, R. (1978). Spermatophores of six eastern North American pyramidellid gastropods and their systematic significance (with the new genus *Boonea*). *Biological Bulletin, Marine Biological Laboratory Woods Hole* 155: 360–382
- Robertson, R. (1980). *Epitonium millicostatum* and *Coralliophila clathrata*: two prosobranch gastropods symbiotic with Indo-Pacific *Palythoa* (Coelenterata: Zoanthidae). *Pacific Science* 34(1): 1–17
- Robertson, R. (1981). Protandry with only one sex change in an *Epitonium* (Ptenoglossa). *The Nautilus* 95(4): 184–186
- Robertson, R. (1983a). Axial shell rib counts as systematic characters in *Epitonium*. *The Nautilus* 97(3): 116–118
- Robertson, R. (1983b). Extraordinarily rapid postlarval growth of a tropical wentletrap (*Epitonium albidum*). *The Nautilus* 97(2): 60–66
- Robertson, R. (1983c). Observations on the life history of the wentletrap (*Epitonium echinaticostum*) in the Bahamas. *The Nautilus* 97(3): 98–103
- Robertson, R. (1983d). Observations on the life history of the wentletrap *Epitonium albidum* in the West Indies. *American Malacological Bulletin* 1: 1–11
- Robertson, R. (1985a). Archaeogastropod biology and the systematics of the genus *Tricolia* (Trochacea: Tricoliidae) in the Indo-West-Pacific. *Monographs of Marine Mollusca* No. 3: 1–103
- Robertson, R. (1985b). Four characters and the higher category systematics of gastropods. *American Malacological Bulletin, Special Edition* No. 1: 1–22
- Robertson, R. (1989). Spermatophores of aquatic non-stylommatophoran gastropods: a review with new data on *Heliacus* (Architectonicidae). *Malacologia* 30: 341–364
- Robertson, R. & Mau-Lastovicka, T. (1979). The ectoparasitism of *Boonea* and *Fargoa* (Gastropoda: Pyramidellidae). *Biological Bulletin, Marine Biological Laboratory Woods Hole* 157: 320–333
- Robertson, R. & Orr, V. (1961). Review of pyramidellid hosts with notes on an *Odostomia* parasitic on a chiton. *The Nautilus* 74: 85–91
- Robertson, R., Scheltema, R.S. & Adams, F.W. (1970). The feeding, larval dispersal, and metamorphosis of *Philippia* (Gastropoda: Architectonicidae). *Pacific Science* 24: 55–65
- Robinson, E. (1960). Observations on the toxoglossan gastropod *Mangelia brachystoma* (Philippi). *Proceedings of the Zoological Society of London* 135: 319–338
- Röckel, D., Korn, W. & Kohn, A.J. (1995). *A Manual of Living Conidae*. Verlag Christa Hemmen: Wiesbaden 358 pp.
- Rohde, K. (1981). Population dynamics of two snail species, *Planaxis sulcatus* and *Cerithium moniliferum*, and their trematode species at Heron Island, Great Barrier Reef. *Oecologia (Heidelberg)* 49: 344–352
- Roller, R.A., Rickett, J.D. & Stickley, W.B. (1995). The hypobranchial gland of the estuarine snail *Stramonita haemastoma canaliculata* (Gray) (Prosobranchia: Muricidae): a light and electron microscopical study. *American Malacological Bulletin* 11: 177–190
- Rosen, N. (1910). Zur Kenntniss der parasitischen Schnecken. *Acta Universitatis Lundensis* (2) 2: 1–67
- Rosenberg, G. (1996a). Anatomy and morphometric analysis of the truncatellid nervous system (Gastropoda: Risssooidea). *Journal of Molluscan Studies* 62: 507–516
- Rosenberg, G. (1996b). Independent evolution of terrestriality in Atlantic truncatellid gastropods. *Evolution* 50:682–693
- Rosenberg, G. & Davis, G.M. (1990). Case 2699. Risssooidea (or Risssoacea) Gray, 1847 (Mollusca, Gastropoda): proposed precedence over Truncatelloidea (or Truncatellacea) Gray, 1840. *Bulletin of Zoological Nomenclature* 47: 104–109
- Rosenberg, G., Kuncio, R.S., Davis, G.M. & Harasewych, M.G. (1994). Ribosomal RNA phylogeny of selected gastropod and unionacean bivalve mollusks. Pp. 111–121 in Harasewych, M.G. & Tillier, S. (eds) *Molecular Techniques and Molluscan Phylogeny*. Proceedings of a Symposium held at the 11th International Malacological Congress, Siena, 1992. *The Nautilus, Supplement* 2
- Rosewater, J. (1969). Gross anatomy and classification of the commensal gastropod, *Caledoniella montrouzieri* Sowerbie, 1869. *The Veliger* 11: 345–350
- Rosewater, J. (1970). The family Littorinidae in the Indo-Pacific. Part I. The subfamily Littorininae. *Indo-Pacific Mollusca* 2: 417–506
- Rosewater, J. (1972). The family Littorinidae in the Indo-Pacific. Part II. The subfamilies Tectariinae and Echininae. *Indo-Pacific Mollusca* 2: 507–533
- Rouse, G.W. & Jamieson, B.G.M. (1987). An ultrastructural study of the spermatozoa of the polychaetes *Eurythoe complanata* (Amphinomidae), *Clymenella* sp. and *Micromaldane* sp. (Maldanidae), with a definition of sperm types in relation to reproductive biology. *Journal of Submicroscopical Cytology* 19: 573–584
- Rubio-Salazar, F. (1990). Skeneidos infra y cirralitorales de las costas del sur y levante Español. *Iberus* 9: 187–202
- Rudman, W.B. (1969). Observations on *Pervicacia tristis* (Deshayes, 1859) and a comparison with other toxoglossan gastropods. *The Veliger* 12: 53–64
- Rumphius, G.E. (1705). *D'Amboinsche Rariteikamer, behelzende eene beschryvinge van allerhande zoo weeke als harde schaalvischen, te weeten raare Krabben, Kreeften, en diergelyke Zeedieren, als mede allerhande Hoornijes en Schulpen, die men in d'Amboinsche Zee vindt: daar beneven zommige Mineraalen, Gesteenten, en soorten van Aarde, die in d'Amboinsche, en zommige omleggende Eilanden gevonden worden*. Amsterdam, 3 vols xxviii 340 pp.
- Rumsey, T.J. (1972). Osmotic and ionic regulation in a terrestrial snail, *Pomatias elegans* (Gastropoda, Prosobranchia) with a note on some tropical Pomatiasidae. *Journal of Experimental Biology* 57: 205–215
- Runham, N.W., Thornton, P.R., Shaw, D.A. & Wayte, R.C. (1969). The mineralisation and hardness of the radular teeth of the limpet, *Patella vulgata* L. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 99: 608–626
- Runnegar, B. (1983). Molluscan phylogeny revisited. *Association of Australasian Paleontologists, Memoir* 1: 121–144
- Runnegar, B. & Pojeta, J. (1985). Origin and diversification of the Mollusca. Pp. 1–57 in Trueman E.R. & Clarke M.R. (eds) *The Mollusca. Vol. 10. Evolution*. Academic Press: New York

15. PROSOBRANCHS

- Russell, F.S. & Colman, J.S. (1935). The zooplankton. IV. The occurrence and seasonal distribution of Tunicata, Mollusca and Coelenterata (Siphonophora). Great Barrier Reef Expedition 1928-1929. *Scientific Reports of the Great Barrier Reef Expedition 1928-29* 2: 235-253
- Russell, H.D. (1960). Heteropods and pteropods as food of the fish genera, *Thunnus* and *Alepisaurus*. *Nautilus* 74: 46-56
- Russell-Hunter, W.D. & Apley, M.L. (1968). Pedal expansion in the naticid snails. II. Labelling experiments using inulin. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 135: 563-573
- Russell-Hunter, W.D. & Russell-Hunter, M.L. (1968). Pedal expansion in the naticid snails. I. Introduction and weighing experiments. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 135: 548-562
- Sacchi, C.F. & Rastelli, M. (1966). *Littorina mariae*, nov. sp.: les différences morphologiques et écologiques entre 'nains' et 'normaux' chez l'espèce *L. obtusata* (L.) (Gastr. Prosobr.) et leur signification adaptative et évolutive. *Atti della Società Italiana Scienze Naturali e del Museo Civile di Storia Naturale, Milano* 105: 351-369
- Safriel, U. (1966). Recent vermetid formation on the Mediterranean shore of Israel. *Proceedings of the Malacological Society of London* 37: 27-34
- Salvini-Plawen, L. von (1972). Zur Morphologie und Phylogenie der Mollusken: die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia (nebst einen Beitrag zur Phylogenie der coelomatischen Räume). *Zeitschrift für Wissenschaftliche Zoologie, Leipzig* 184: 205-394
- Salvini-Plawen, L. von (1980). A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* 19: 249-278
- Salvini-Plawen, L. von (1981). On the origin and evolution of the Mollusca. *Atti dei convegni Lincei* 49: 235-293
- Salvini-Plawen, L. von (1988). The structure and function of molluscan digestive systems. Pp. 301-379 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca. Vol. 11. Form and Function*. Academic Press : Orlando
- Salvini-Plawen, L. von (1990). Origin, phylogeny and classification of the phylum Mollusca. *Iberus* 9: 1-33
- Salvini-Plawen, L. von & Haszprunar, G. (1987). The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *Journal of Zoology, London* 211: 747-770
- Sasaki, T. (1992). Taxonomic study of the genus *Notoacmea* (Gastropoda: Lottiidae) in Japan. Graduation thesis, Laboratory of Invertebrate Zoology, Tokyo University of Fisheries
- Sasaki, T. & Okutani, T. (1993a). New genus *Nipponacmea* (Gastropoda, Lottiidae): a revision of Japanese limpets hitherto allocated in *Notoacmea*. *Venus* 52: 1-40
- Sasaki, T. & Okutani, T. (1993b). Anatomy and systematic position of *Yayoiacmea*, a new genus for Japanese tiny limpet "*Collisella*" *oyamai* Habe, 1955 (Gastropoda: Lottiidae). *Venus* 52: 193-209
- Sasaki, T. & Okutani, T. (1994). An analysis on "*Collisella heroldi*" complex (Gastropoda: Lottiidae), with description of three new species. *Venus* 53: 251-285
- Savrujev, V.M. (1985). Remarkable conformity in the morphology of two gastropod species. *La Conchiglia* 198-199: 12-13
- Schäfer, H. (1952). Ein Beitrag zur Ernährungsbiologie von *Bithynia tentaculata* L. (Gastropoda Prosobranchia). *Zoologischer Anzeiger* 148: 299-303
- Schäfer, H. (1953). Beiträge zur Ernährungsbiologie einheimischer Süßwasserprosobranchier. *Zeitschrift für Morphologie und Oekologie der Tiere* 41: 247-264
- Schaefer, K. (1996). Development and homologies of the anal gland in *Haminaea navicula* (Da Costa, 1778) (Opisthobranchia, Bullomorpha). Pp. 249-260 in Taylor, J.D. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : Oxford
- Scheibling, R.E. & Black, R. (1993). The ecology of the giant limpet *Patella laticostata* on intertidal limestone platforms at Rottnest Island, Western Australia. Pp. 565-581 in Wells, F.E. (ed.) *The Marine Flora and Fauna of Rottnest Island, Western Australia, Vol. 2. Fifth International Marine Biological Workshop, Rottnest Island, Western Australia, Australia*. Western Australian Museum : Perth
- Scheibling, R.E., Evans, T., Mulvey, P., Lebel, T., Williams, D. & Holland, S. (1990). Commensalism between an epizoic limpet *Patelloida nigrosulcata*, and its gastropod hosts *Haliotis roei* and *Patella laticostata*, on intertidal platforms off Perth, Western Australia. *Australian Journal of Marine and Freshwater Research* 41: 647-655
- Scheltema, R.S. (1956). The effect of substrate on the length of the planktonic existence in *Nassarius obsoleta*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 111: 312
- Scheltema, R.S. (1966). Evidence for trans-Atlantic transport of gastropod larvae belonging to the genus *Cymatium*. *Deep Sea Research* 13: 83-95
- Scheltema, R.S. (1968). Dispersal of larvae by equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. *Nature* 217: 1159-1162
- Scheltema, R.S. (1971). Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 140: 284-322
- Scheltema, R.S. (1972). Eastward and westward dispersal across the tropical Atlantic Ocean of larvae belonging to the genus *Bursa* (Prosobranchia, Mesogastropoda, Bursidae). *Internationale Revue der Gesamten Hydrobiologie* 57: 863-873
- Scheltema, R.S. (1986a). Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among central Pacific islands. *Bulletin of Marine Science* 39: 241-256
- Scheltema, R.S. (1986b). On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* 39: 290-322
- Scheltema, R.S. (1986c). Epipelagic meroplankton of tropical seas: its role for the biogeography of sublittoral invertebrate species. *UNESCO Technical Papers in Marine Science* 49: 242-249
- Scheltema, R.S. (1988). Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the East Pacific barrier. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 174: 145-152
- Scheltema, R.S. & Williams, I.P. (1983). Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and western Pacific mollusks. *Bulletin of Marine Science* 33: 545-565
- Scheltema, R.S., Williams, I.P. & Tharpe, J. (1989). Differences in spatial distribution of veliger larvae belonging to *Litiopa melanostoma* and *Alaba incerta* (Prosobranchia: Litiopidae) in the warm temperate and tropical North Atlantic Ocean. *Journal of Molluscan Studies* 55: 139-143
- Schepman, M.M. (1908). Prosobranchia (excluding Heteropoda and parasitic Prosobranchia). Part 1: Rhipidoglossa and Docoglossa. With an appendix by Prof. R. Bergh [Pectinobranchiata]. *Siboga Expedition* 49: 1-108 9 pls.
- Schilder, F.A. (1927). Revision der Cypraeacea (Moll. Gastr.). *Archiv Naturgeschichte* 91A: 1-171
- Schilder, F.A. (1932). The living species of Amphiperatinae. *Proceedings of the Malacological Society of London* 20: 46-64
- Schilder, F.A. (1933). Monograph of the subfamily Eratoinae. *Proceedings of the Malacological Society of London* 20: 244-284
- Schilder, F.A. (1936). Anatomical characters of the Cypraeacea which confirm the conchological classification. *Proceedings of the Malacological Society of London* 22: 75-112
- Schilder, F.A. (1965). The geographical distribution of cowries (Mollusca: Gastropoda). *The Veliger* 7: 171-183
- Schilder, F.A. & Schilder, M. (1938-39). Prodrôme of a monograph on living Cypraeidae. *Proceedings of the Malacological Society of London* 23: 119-231
- Schilder, M. & Schilder, F.A. (1962). Sex and size. *The Cowry* 1(4): 50-52

- Schilder, M. & Schilder, F.A. (1971). A catalogue of living and fossil cowries. Taxonomy and Bibliography of Triviacea and Cypraea (Gastropoda, Prosobranchia). *Mémoires de l'Institut Royal des Sciences Naturelle de Belgique, 2nd Série* 85:1-246
- Schmekel, L. (1985). Aspects of evolution within the opisthobranchs. Pp. 221-267 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca. Vol. 10. Evolution*. Academic Press : San Diego
- Schneider, E. (1920). Das Darmsystem von *Cyclophorus ceylanicus* [Fauna et Anatomia ceylanica, No. 5]. *Jenaische Zeitschrift für Naturwissenschaft* 57: 1-86
- Schultz, M.C. (1983). A correlated light and electron microscopic study of the structure and secretory activity of the accessory salivary glands of the marine gastropods, *Conus flavidus* and *C. vexillum* (Neogastropoda, Conacea). *Journal of Morphology* 176: 89-111
- Seapy, R.R. (1974). Distribution and abundance of the epipelagic heteropod mollusk *Carinaria japonica* in the waters off southern California. *Marine Biology* 24: 243-250
- Seapy, R.R. (1980). Predation by the epipelagic heteropod mollusc *Carinaria cristata* forma *japonica*. *Marine Biology* 60: 137-146
- Seapy, R.R. (1985). The pelagic genus *Pterotrachea* (Gastropoda: Heteropoda) from Hawaiian waters: a taxonomic review. *Malacologia* 26: 125-135
- Seapy, R.R. (1990). The pelagic family Atlantidae (Gastropoda: Heteropoda) from Hawaiian waters: a faunistic survey. *Malacologia* 32: 107-130
- Seapy, R.R. & Young, R.E. (1986). Concealment in epipelagic pterotracheid heteropods (Gastropoda) and cranchiid squids (Cephalopoda). *Journal of Zoology, London* 210(A): 137-147
- Seaward, D.R. (1988). Locomotion of *Truncatella subcylindrica*. *Journal of Conchology* 33: 49-53
- Selmi, M.G. & Giusti, F. (1983). The atypical spermatozoon of *Theodoxus fluviatilis* (Gastropoda: Prosobranchia). *Journal of Ultrastructure Research* 84: 173-181
- Seshaiya, R.V. (1934). Anatomy of *Paludomus transchaurica* (Gmelin). *Records of the Indian Museum* 36: 185-212
- Seshaiya, R.V. (1940). A free larval stage in the life history of a fluviatile gastropod. *Current Science* 9: 331-332
- Sewell, S. (1924). Observations on growth in certain molluscs and on changes correlated with growth in the radula of *Pyraruz palustris*. *Records of the Indian Museum* 26: 529-548
- Shabica, S.V. (1971). The general ecology of the antarctic limpet *Patinigera polaris*. *Antarctic Journal of the United States* 6: 160-162
- Shank, P. (1969). The timorous carrier shell; close observations of *Xenophora conchyliphora* Born. *New York Shell Club Notes* 151: 5-7
- Sharman, M. (1956). Note on *Capulus ungaricus* (L.). *Journal of the Marine Biological Association of the United Kingdom* 35: 445-450
- Shaw, H.O.N. (1909). Notes on the genera *Cypraea* and *Trivia*. *Proceedings of the Malacological Society of London* 8: 188-313
- Shaw, H.O.N. (1914). On the anatomy of *Conus tulipa* and *Conus textile*, Linn. *Quarterly Journal of Microscopical Science* 60: 1-60
- Sheldon, F. & Walker, K.F. (1993a). Morphological variation in Australian species of *Notopala* (Gastropoda: Viviparidae). *Journal of the Malacological Society of Australia* 14: 59-71
- Sheldon, F. & Walker, K.F. (1993b). Pipelines as a refuge for freshwater snails. *Regulated Rivers: Research and Management* 8: 295-300
- Shenk, M.A. & Karlson, R.H. (1986). Colonization of a shell resource by calyptraeid gastropods: tests of habitat selection and preemption models. *Journal of Experimental Marine Biology and Ecology* 99: 79-89
- Shepherd, S.A. (1973). Studies on southern Australian abalone (genus *Haliotis*). Ecology of five sympatric species. *Australian Journal of Marine and Freshwater Research* 24: 217-257
- Shepherd, S.A. & Steinberg, P.D. (1992). Food preferences of three Australian abalone species with a review of the algal food of abalone. Pp. 169-181 in Shepherd, S.A., Tegner, M.J. & Guzmán del Prío, S.A. (eds) *Abalone of the World*. Fishing News Books : Oxford
- Sheridan, R., Van Mol, J.J. & Bouillon, J. (1973). Etude morphologique du tube digestif de quelques Turridae (Mollusca-Gastropoda-Prosobranchia-Toxoglossa) de la région de Roscoff. *Cahiers de Biologie Marine* 14: 159-188
- Shileyko, A.A. (1977). The symmetry of the Docoglossa and the problem of the origin of the order (Mollusca: Gastropoda) (in Russian). *Bulletin of the Moscow Naturalist's Society, Biological Series* 81: 60-65 (English summary in *The Veliger* 21: 494)
- Shimek, R.L. (1975). The morphology of the buccal apparatus of *Oenopota levidensis* (Gastropoda, Turridae). *Zeitschrift für Morphologie der Tiere* 80: 59-96
- Shimek, R.L. (1983a). The biology of northeastern Pacific Turridae. II. *Oenopota*. *Journal of Molluscan Studies* 49: 146-163
- Shimek, R.L. (1983b). The biology of northeastern Pacific Turridae. I. *Ophiidermella*. *Malacologia* 23: 281-312
- Shimek, R.L. (1983c). The biology of the northeastern Pacific Turridae. III. The habitat and diet of *Kurtziella plumbea* (Hinds, 1843). *The Veliger* 26: 10-17
- Shimek, R.L. (1986). The biology of the northeastern Pacific Turridae. V. Demersal development, synchronous settlement and other aspects of the larval biology of *Oenopota levidensis*. *International Journal of Invertebrate Reproduction and Development* 10: 313-333
- Shimek, R.L. & Kohn, A.J. (1981). Functional morphology and evolution of the toxoglossan radula. *Malacologia* 20: 423-438
- Shuto, T. (1983). New turrid taxa from the Australian waters. *Memoirs of the Faculty of Sciences of Kyushu University, Series D, Geology* 25: 1-26
- Signor, P.W. III (1983). Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. *Malacologia* 23: 313-320
- Signor, P.W. & Kat, P.W. (1984). Functional significance of columellar folds in turritelliform gastropods. *Journal of Paleontology* 58: 210-216
- Simone, L.R.L. de (1996). *Addisonia enodis*, a new species of Addisoniidae (Mollusca, Archaeogastropoda) from the Southern Brazilian coast. *Bulletin of Marine Science* 58: 775-785
- Simpson, R.D. (1976). Physical and biotic factors limiting the distribution and abundance of littoral molluscs on Macquarie island (sub-antarctic). *Journal of Experimental Marine Biology and Ecology* 21: 11-49
- Simpson, R.D. (1985). Relationship between allometric growth, with respect to shell height, and habitats for two patellid limpets, *Nacella (Patinigera) macquariensis* Finlay, 1927, and *Cellana tramoserica* (Holten, 1802). *The Veliger* 28: 18-27
- Simroth, H. (1895). Die Gastropoden der Plankton-Expedition. *Ergebnisse der Atlantic Plankton-Expedition* 2: 1-206 Velutinidae
- Simroth, H. (1910). Some remarks with regard to Professor Bourne's monograph on the Neritidae. *Proceedings of the Malacological Society of London* 9: 27-33
- Simroth, H. (1911). Die Gastropoden des nordischen Plankton. *Nordisches Plankton* 5(13): 1-36
- Skilleter, G.A. (1991). Distribution, abundance and size-structure of cerithiid gastropods in sediments at One Tree Reef, southern Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 151: 185-207
- Skilleter, G.A. (1992). Recruitment of cerithiid gastropods (*Rhinoclavis* spp.) in sediments at One Tree Reef, Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 156: 1-21
- Skilleter, G.A. & Underwood, A.J. (1993). Effects of habitat composition on recruitment of cerithiid gastropods in sediments at One Tree Reef, Great Barrier Reef. *Marine Ecology Progress Series* 93: 155-163

15. PROSOBRANCHS

- Skoog, G. (1978). Influence of natural food items on growth and egg production in brackish water populations of *Lymnaea peregra* and *Theodoxus fluviatilis* (Mollusca). *Oikos* 31: 340–348
- Skwarko, S.K. (1966). Cretaceous stratigraphy and palaeontology of the Northern Territory. *Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 73: 1–133
- Slack-Smith, S. (1983). Australia's split shell. *Australian Shell News* 43: 8
- Sleurs, W.J. (1984). The marine microgastropods from the northern coast of Papua New Guinea (Mollusca: Gastropoda). 1. Family: Omalogyridae (with description of two new species). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 55: 1–11
- Sleurs, W.J. (1985a). *Ammonicera angulata* sp. nov. from Laing Island Papua New Guinea, with comments on the genus *Ammonicera* Vayssière, 1893 (Mollusca: Gastropoda). *Annales de la Société Royale Zoologique de Belgique* 115: 177–181
- Sleurs, W.J. (1985b). Marine microgastropods from the Republic of the Maldives. 1. Genus *Ammonicera* Vayssière 1893, with description of four new species (Prosobranchia: Omalogyridae). *Basteria* 49: 19–27
- Sleurs, W.J.M. (1993). A revision of the Recent species of *Rissoina* (*Moerchiella*), *R. (Apataxia)*, *R. (Alinzebia)* and *R. (Pachyrissoina)* (Gastropoda: Rissoidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 63: 71–135
- Sly, F.L. (1984). Genetic variation, adaptive strategies and systematic relationships of five species of limpet of the family Acmaeidae. MSc thesis, Marine Science, University of California, Santa Cruz, California
- Smith, B.J. & Kershaw, R.C. (1979). *Field Guide to the Non-Marine Molluscs of South Eastern Australia*. Australian National University Press : Canberra x 285 pp.
- Smith, B.J. (1992). Non-Marine Mollusca. In Houston, W.W.K. (ed.) *Zoological Catalogue of Australia*. Vol. 8. AGPS : Canberra xii 408 pp.
- Smith, B.J., Black, J.H. & Shepherd, S.A. (1989). Molluscan egg masses and capsules. Pp. 841–891 in Shepherd, S.A. & Thomas, I.M. (eds) *Marine Invertebrates of South Australia. Part II*. South Australian Government Printer : Adelaide
- Smith, C.R., Kukert, H., Wheatcroft, R.A., Jumars, P.A. & Deming, J.W. (1989). Vent fauna on whale remains. *Nature, London* 314: 27–28
- Smith, D.A.S. (1973). The population biology of *Lacuna pallidula* (da Costa) and *Lacuna vineta* (Montagu) in north-east England. *Journal of the Marine Biological Association of the United Kingdom* 53: 493–520
- Smith, E.A. (1886). Description of a new species of *Lamellaria* from South Australia. *Annals and Magazine of Natural History* (5) 58: 270–271
- Smith, E.A. (1904). Natural history notes from H.M. Indian Marine Survey Steamer *Investigator*, commander T.H. Heming, R.N. Series 3, No. 1. On Mollusca from the Bay of Bengal and the Arabian Sea. *Annals and Magazine of Natural History, Series 7* 13 (79): 453–473
- Smith, E.A. (1908). The known Recent species of *Vanikoro* Quoy and Gaimard. *Proceedings of the Malacological Society* 8: 104–117
- Smith, E.H. (1967a). The proboscis and oesophagus of some British turrids. *Transactions of the Royal Society of Edinburgh* 67: 1–22
- Smith, E.H. (1967b). The neogastropod stomach, with notes on the digestive diverticula and intestine. *Transactions of the Royal Society of Edinburgh* 67: 23–42
- Smith, E.H. (1967c). The reproductive system of the British Turridae (Gastropoda: Toxoglossa). *The Veliger* 10: 176–187
- Smith, E.H. (1967d). Two new species of British turrids. *The Veliger* 10: 1–4
- Smith, F.G.W. (1935). The development of *Patella vulgata*. *Philosophical Transactions of the Royal Society of London, Series B* 225: 95–125
- Smith, M. (1953). *An illustrated catalog of the Recent species of rock shells. Muricidae, Thaisidae and Coralliophilidae*. Tropical Laboratory : Windermere, Florida 84 pp. 23 pls
- Smith, T.B. (1984). Ultrastructure and function of the proboscis in *Melanella alba* (Gastropoda, Eulimidae). *Journal of the Marine Biological Association of the United Kingdom* 64: 503–512
- Snyder, N.F.R. & Snyder, H.A. (1971). Pheromone-mediated behavior of *Fasciolaria tulipa*. *Animal Behaviour* 19: 257–268
- Soemodihardjo, S. & Kastoro, W. (1977). Notes of the *Terebralia palustris* (Gastropoda) from the coral islands in the Jakarta Bay area. *Marine Research in Indonesia* No. 18: 131–148
- Sohl, N.F. (1963). New gastropod genera from the late Upper Cretaceous of the East Gulf Coastal Plain. *Journal of Paleontology* 37: 747–757
- Sohl, N.F. (1987). Cretaceous gastropods: contrasts between Tethys and the temperate provinces. *Journal of Paleontology* 61: 1085–1111
- Solem, A. (1959). Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana Zoology* 43: 1–359
- Solem, A. (1978). Classification of the land Mollusca. Pp. 49–97 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 2A. Systematics, Evolution and Ecology*. Academic Press : London
- Solem, A. (1988). Non-camaenid land snails of the Kimberley and Northern Territory, Australia. I. Systematics, affinities and ranges. *Invertebrate Taxonomy* 2: 455–604
- Solem, A., Girardi, E.L., Slack-Smith, S. & Kendrick, G.W. (1982). *Austroassiminea lethra*, gen. nov., sp. nov., a rare and endangered prosobranch snail from south-western Australia (Mollusca: Prosobranchia: Assimineidae). *Journal of the Royal Society of Western Australia* 65(4): 119–129
- Solem, A. & Yochelson, E.L. (1979). North American Paleozoic land snails, with a summary of other Paleozoic non-marine snails. *United States Geological Survey, Professional Paper* 1072: 1–42
- Soong, K. & Chen, J.-L. (1991). Population structure and sex-change in the coral inhabiting snail *Coralliophila violacea* at Hsiao-Liuchiu, Taiwan. *Marine Biology* 111: 81–86
- Southgate, T. (1982). The biology of *Barleeia unifasciata* (Gastropoda: Prosobranchia) in red algal turfs in S.W. Ireland. *Journal of the Marine Biological Association of the United Kingdom* 62: 461–468
- Speed, E. (1969). Prehistoric shell collectors. *South African Archaeological Bulletin* 24: 193–196
- Spengel, J.W. (1881). Die Geruchsorgane und das Nervensystem der Mollusken. Ein Beitrag zur Erkenntnis der Einheit des Molluskentypus. *Zeitschrift für Wissenschaftliche Zoologie* 35: 333–383
- Spengler, H.A. & Kohn, A.J. (1995). Comparative external morphology of the *Conus osphradium* (Mollusca: Gastropoda). *Journal of Zoology, London* 235: 439–453
- Spoel, van der S. (1972). Notes on the identification and speciation of Heteropoda (Gastropoda). *Zoologische Mededeelingen, Leiden* 47: 545–560
- Spoel, van der S. (1976). *Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda)*. Bohn, Scheltema & Holkema : Utrecht 484 pp.
- Spoel, van der S., Newman, L.J. & Estep, K.W. (eds) (1997). *Pelagic Molluscs of the World*. Expert-Center for Taxonomic Identification, Amsterdam. World Biodiversity Database. CD-ROM Series, ISBN 3-540-14507-9
- St Jean, K. (1972). Antique collectors of the sea. The *Xenophora*. *Echo* 5: 42–43
- Staiger, H. (1950). Zur Determination der Nöhreier bei Prosobranchiern. *Revue Suisse de Zoologie* 57: 496–503
- Staiger, H. (1951). Cytologische und morphologische Untersuchungen zur Determination der Nöhreier bei Prosobranchiern. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 35: 495–549
- Stanley, S.M. (1982). Gastropod torsion: predation and the opercular imperative. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 164: 95–107
- Starmühlner, F. (1969). Die Gastropoden der Madagassischen Binnengewässer. *Malacologia* 8: 1–434

- Starmühlner, F. (1970). Die Mollusken der Neukaledonischen binnengewässer. *Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer, Série Hydrobiologie* 4: 3–128
- Starmühlner, F. (1976). Beiträge zur Kenntnis der Süßwasser-Gastropoden pazifischer Inseln. *Annalen des Naturhistorischen Museums in Wien* 80: 473–656
- Starmühlner, F. (1992). The species of the family Thiaridae of isolated Indo-Pacific Islands. Pp. 363–366 in Giusti, F. & Manganelli, G. (eds) *Eleventh International Malacological Congress, Siena Italy* (Abstracts). University of Siena and Unitas Malacologica : Siena
- Starmühlner, F. (1993). Ergebnisse der österreichischen Tonga-Samoa Expedition 1985 des Instituts für Zoologie der Universität Wien: Beiträge zur Kenntnis der Süß- und Brackwasser-Gastropoden der Tonga- und Samoa-Inseln (SW-Pazifik). *Annalen des Naturhistorischen Museums in Wien, Serie B Botanik und Zoologie* 94–95: 217–306
- Starobogatov, Y.I. (1988). On the systematic position of the genus *Glacidorbis* (Gastropoda incertae sedis). *Proceedings of the Zoological Institute, Leningrad* 176: 78–84 [in Russian]
- Starobogatov, Y.I., Sitnikova, T.Y. & Zatravkin, M.N. (1989). Family Irvadiidae (Gastropoda, Pectinibranchia) and its representatives in brackish waters of the USSR. *Zoologicheskii Zhurnal* 68: 35–44
- Stasek, C.R. & McWilliams, W.R. (1973). The comparative morphology and evolution of the molluscan mantle edge. *The Veliger* 16: 1–19
- Steadman, W.R. & Cotton, B.C. (1946). A key to the classification of the cowries (Cypraeidae). *Records of the South Australian Museum* 8: 503–528
- Steneck, R.S. & Watling, L. (1982). Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. *Marine Biology* 68: 299–319
- Stilwell, J.D. & Zinsmeister, W.J. (1992). Molluscan systematics and biostratigraphy. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *Antarctic Research* 55: 1–192
- Stirling, H.P. (1977). Effects of a spill of marine diesel oil on the rocky shore fauna of Lamma Island Hong Kong. *Environmental Pollution* 12: 93–117
- Stoddart, J.A. (1982). Western Australian viviparids (Prosobranchia: Mollusca). *Journal of the Malacological Society of Australia* 5: 167–173
- Stoddart, J.A. (1983). The accumulation of genetic variation in a parthenogenetic snail. *Evolution* 37: 546–554
- Stoddart, J.A. (1985). Analysis of species lineages of some Australian thiarids (Thiaridae, Prosobranchia, Gastropoda) using the evolutionary species concept. *Journal of the Malacological Society of Australia* 7: 7–16
- Stoner, A.W. & Lally, J. (1994). High-density aggregation in queen conch *Strombus gigas*: formation, patterns, and ecological significance. *Marine Ecology Progress Series* 106: 73–84
- Stoner, A.W., Lipcius, R.N., Marshall, L.S. Jr & Bardales, A.T. (1988). Synchronous emergence and mass migration in juvenile queen conch. *Marine Ecology Progress Series* 49: 51–55
- Storch, V. & Welsch, U. (1969). Über Aufbau und Innervation der Kopfanhänge der prosobranchen Schnecken. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 102: 419–431
- Struhsaker, J.W. & Costlow, J.D. (1968). Larval development of *Littorina picta* (Prosobranchia, Mesogastropoda), reared in the laboratory. *Proceedings of the Malacological Society of London* 38: 153–160
- Struhsaker, J.W. (1966). Breeding, spawning, spawning periodicity and early development in the Hawaiian *Littorina*: *L. pintado* (Wood), *L. picta* (Philippi) and *L. scabra* (Linné). *Proceedings of the Malacological Society of London* 37: 137–166
- Stuber, R.A. & Lindberg, D.R. (1989). Is the radula of living monoplacophorans primitive? *Abstract of Program, Annual Meeting. Geological Society of America* 21(7): A289
- Stützel, R. (1984). Anatomische und ultrastrukturelle Untersuchungen an der Napfschnecke *Patella* L. unter besonderer Berücksichtigung der Anpassung an den Lebensraum. *Zoologica* 46: 1–54
- Suter, H. (1908). Additions to the marine molluscan fauna of New Zealand, with descriptions of new species. *Proceedings of the Malacological Society of London* 8: 22–42, pls 2–3
- Sutherland, S.K. (1983). Venomous Cone Shells. Pp. 389–399 in *Australian Animal Toxins*. Oxford University Press : Melbourne xiii 527 pp.
- Swainson, W.S. (1840). *A Treatise on Malacology, or shells and shellfish*. In *Lardner's Encyclopedia*. Spottiswoode : London 419 pp.
- Szal, R. (1971). 'New' sense organ of primitive gastropods. *Nature* 229: 490–492
- Taki, I. (1956). Anatomical study of Japanese Epitoniidae (1). *Epitonium, Amaea and Papyriscala*. *Bulletin of the National Science Museum, Tokyo* 3: 71–79, pls 13–17
- Taki, I. (1957). Anatomical study of Japanese Epitoniidae (2). *Gyroscala and Acutiscala*. *Bulletin of the National Science Museum, Tokyo* 3: 176–182, pls 34–38
- Tate, R. (1888). The gastropods of the older Tertiary of Australia. *Transactions of the Royal Society of South Australia* 10: 91–176
- Tate, R. (1889). The gastropods of the older Tertiary of Australia. (Part II.) *Transactions of the Royal Society of South Australia* 11: 116–174
- Tate, R. (1893a). Unrecorded genera of the Older Tertiary fauna of Australia, including diagnoses of some new genera and species. *Journal and Proceedings of the Royal Society of New South Wales* 27: 167–196
- Tate, R. (1893b). The gastropods of the older Tertiary of Australia. *Transactions of the Royal Society of South Australia* 17: 316–345
- Tate, R. & Brazier, J. (1882). Check list of the fresh-water shells of Australia. *Proceedings of the Linnean Society of New South Wales* 6: 552–569
- Tate, R. & May, W.L. (1900). Descriptions of new genera and species of Australian Mollusca (chiefly Tasmanian). *Transactions of the Royal Society of South Australia* 24: 90–103
- Taylor, D.W. & Sohl, N.F. (1962). An outline of gastropod classification. *Malacologia* 1: 7–32
- Taylor, D.W. (1966). A remarkable snail fauna from Coahuila, Mexico. *The Veliger* 9: 152–228
- Taylor, J.B. (1975). Planktonic prosobranch veligers of Kaneohe Bay. PhD dissertation, University of Hawaii, Honolulu
- Taylor, J.D. (1976). Habitats, abundance and diets of Muricacean gastropods at Aldabra Atoll. *Journal of the Linnean Society, Zoology* 59: 155–193
- Taylor, J.D. (1977). Food and habitats of predatory gastropods on coral reefs. *Report of the Underwater Association, (N.S.)* 2: 17–34
- Taylor, J.D. (1978a). The diet of *Buccinum undatum* and *Neptunea antiqua* (Gastropoda: Buccinidae). *Journal of Conchology, London* 29: 309–318
- Taylor, J.D. (1978b). Habitats and diet of predatory gastropods at Addu Atoll, Maldives. *Journal of Experimental Marine Biology and Ecology* 31: 83–103
- Taylor, J.D. (1983). The food of coral-reef *Drupa* (Gastropoda). *Zoological Journal of the Linnean Society of London* 78: 299–316
- Taylor, J.D. (1984). The diet of Indo-Pacific *Vasum* (Gastropoda: Vasidae). *Journal of Conchology* 31: 375–382
- Taylor, J.D. (1985). The anterior alimentary system and diet of *Turricula nelliiae spurius* (Gastropoda: Turridae). Pp. 175–190 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and Southern China 2. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 6–24 April 1983*. Hong Kong University Press : Hong Kong
- Taylor, J.D. (1989). The diet of coral-reef Mitridae (Gastropoda) from Guam; with a review of other species of the family. *Journal of Natural History* 23: 261–278
- Taylor, J.D. (1990). The anatomy of the foregut and relationships in the Terebridae. *Malacologia* 32: 19–34

- Taylor, J.D., Kantor, Y.I. & Sysoev, A.V. (1993). Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (=Toxoglossa) (Gastropoda). *Bulletin of the British Museum (Natural History)*, London 59: 125–170
- Taylor, J.D. & Miller, J.A. (1989). The morphology of the osphradium in relation to feeding habits in meso- and neogastropods. *Journal of Molluscan Studies* 55: 227–237
- Taylor, J.D., Morris, N.J. & Taylor, C.N. (1980). Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology (Durham)* 23: 375–409
- Taylor, J.D. & Morris, N.J. (1988). Relationships of neogastropods. Pp. 167–179 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Taylor, J.D. & Reid, D.G. (1990). Shell microstructure and mineralogy of the Littorinidae: ecological and evolutionary significance. *Hydrobiologia* 193: 199–215
- Tenison-Woods, J.E. (1878). On some new marine Mollusca. *Transactions of the Royal Society of Victoria* 14: 55–65
- Tenison-Woods, J.E. (1879). On some Tertiary fossils from Muddy Creek, Western Victoria. *Proceedings of the Linnean Society of New South Wales* 3: 222–240
- Tenison-Woods, J.E. (1882). *The Fish and Fisheries of New South Wales*. Government Printer: Sydney ix 213 pp.
- Tenison-Woods, J.E. (1888). On the anatomy and life history of Mollusca peculiar to Australia. *Journal and Proceedings of the Royal Society of New South Wales* (1888) 22: 106–187
- Tesch, J.J. (1906). Die Heteropoden der 'Siboga' Expedition. *Siboga Report* 51: 1–112
- Tesch, J.J. (1949). Heteropoda. *Dana Report* 34: 1–53
- Thiele, J. (1903). Die Anatomie und systematische Stellung der Gattung *Cocculina*. Die beschalteten Gastropoden der deutschen Tiefsee Expedition 1898–1899. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition "Valdivia"* 7: 147–179, pls 6–9
- Thiele, J. (1908). Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross" ... XV. Ueber die Anatomie und systematische Stellung von *Bathysciadium*, *Lepetella* und *Addisonia*. *Bulletin of the Museum of Comparative Zoology* 52: 81–90, pls 1–2
- Thiele, J. (1909). Cocculinoidea und die Gattungen *Phenacolepas* und *Titiscania*. *Systematisches Conchylien Cabinet von Martini & Chemnitz* 2: 1–48, pls 1–6
- Thiele, J. (1910). Über die Anatomie von *Hydrocena cattaroensis* Pf. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 32: 351–358
- Thiele, J. (1912). Die Antarktischen Schnecken und Muscheln. *Deutschen Südpolar Expedition 1901–1903*, 13, *Zoology* 5: 183–285
- Thiele (1924). Über die Sytematik der Columbellen. *Archiv für Molluskenkunde, Frankfurt* 56: 200–210
- Thiele, J. (1925a). Prosobranchia. Pp. 40–94 in Kükenthal, W. & Krumbach, T. (eds) *Handbuch der Zoologie*. Vol. 5. Walter de Gruyter: Berlin
- Thiele, J. (1925b). Gastropoda der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition* 21: 158–268
- Thiele, J. (1927). Über die schneckenfamilie Assimineidae. *Zoologische Jahrbücher, Abteilung für Systematik* 53: 113–146
- Thiele, J. (1928a). Revision des Systems der Hydrobiiden und Melaniiden. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 55: 351–402
- Thiele, J. (1928b). Über ptenoglosse Schnecken. *Zeitschrift für Wissenschaftliche Zoologie* 132: 73–94
- Thiele, J. (1929–1935). *Handbuch der Systematischen Weichtierkunde*. Gustav Fischer: Jena Vol. 1 vi pp. 1–778; Vol. 2 v pp. 779–1134
- Thiem, H. (1917). Beiträge zur Phylogenie der Docoglossen. II. Die Anatomie und Phylogenie der Monobranchen (Akmäiden und Scurriiden nach der Sammlung Plates). *Jenaische Zeitschrift für Naturwissenschaften* 54: 405–630
- Thiriou-Quievreux, C. (1967). Descriptions de quelques vèligères planctoniques de gastéropodes. *Vie et Milieu* 18: 303–315
- Thiriou-Quievreux, C. (1969). Organogenèse larvaire du genre *Atlanta* (Mollusque, Hétéropode). *Vie et Milieu, Série A* 20: 347–395
- Thiriou-Quievreux, C. (1973). Heteropoda. *Oceanography and Marine Biology Annual Review* 11: 237–261
- Thiriou-Quievreux, C. (1977). Particularité de l'appareil génital de quelques espèces de Rissoidae (Mollusca, Mesogastropoda). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences Paris Série D* 285: 779–781
- Thomas, F.J.M. & Kohn, A.J. (1990). Trophic roles of co-occurring species of *Drupa* (Gastropoda: Muricidae) at Enewetak Atoll. *Journal of Molluscan Studies* 56: 57–62
- Thompson, F.G. (1968). *The aquatic snails of the family Hydrobiidae of peninsular Florida*. University of Florida Press: Gainesville
- Thompson, F.G. (1969). Some Mexican and Central American land snails of the family Cyclophoridae. *Zoologica, New York* 54: 35–77
- Thompson, F.G. (1980). Proserpinoid land snails and their relationships within the Archaeogastropoda. *Malacologia* 20: 1–33
- Thompson, T.E. (1961). Acid secretion in British cowries. *Proceedings of the Malacological Society of London* 34: 210–211
- Thompson, W.F. (1912). The protoconch of *Acmaea*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 64: 540–544
- Thorson, G. (1932). Die Lamschnecken-Fauna von Val di Genova in Judicarien (Süd-Tirol) und ihre zoogeographische Stellung. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 92: 227–267
- Thorson, G. (1935). Studies on the egg-capsules and development of Arctic marine Prosobranchs. *Meddelelser om Grønland* 100: 1–71
- Thorson, G. (1940). Studies on the egg masses and larval development of Gastropoda from the Iranian Gulf. *Danish Scientific Investigations in Iran* 2: 159–238
- Thorson, G. (1946). Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Meddelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser, Serie Plankton* 4: 1–523
- Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25: 1–45
- Thorson, G. (1965). A neotenus dwarf form of *Capulus ungaricus* (L.) (Gastropoda: Prosobranchia) commensalistic on *Turritella communis* Risso. *Ophelia* 2: 175–210
- Thorson, G. (1967). *Clanculus bertheloti* d'Orbigny, 1839: eine brutpflegende prosobranchiate Schnecke aus der Brandungszone von Tenerifa. *Zeitschrift für Morphologie und Ökologie der Tiere* 60: 162–175
- Tielecke, H. (1940). Anatomie, Phylogenie und Tiergeographie der Cyclophoriden. *Archiv für Naturgeschichte* 9: 317–371
- Tillier, S. (1981). Clines, convergence and character displacement in New Caledonian diplommatinids (land prosobranchs). *Malacologia* 21: 177–208
- Tillier, S., Masselot, M., Guerdoux, J. & Tillier, A. (1994). Monophyly of major gastropod taxa tested from partial 28S rRNA sequences, with emphasis on Euthyneura and hot-vent limpets Peltospiroidea. *Nautilus, Supplement* 2: 122–140
- Tillier, S., Masselot, M., Hervé, P. & Tillier, A. (1992). Phylogénie moléculaire des Gastropoda (Mollusca) fondée sur le séquençage partiel de l'ARN ribosomique 28S. *Compte Rendu Académie de Sciences, Paris, série 3* 314: 79–85
- Tochimoto, T. (1967). Comparative histochemical study on the dimorphic spermatozoa of the Prosobranchia with special reference to polysaccharides. *Science Report of the Tokyo Kyoiku Daigaku, Section B* 13: 75–109
- Tokioka, T. (1955). Shells of Atlantidae (Heteropoda) collected by the "Soyo Maru" in the southern waters of Japan. *Publications of the Seto Marine Biology Laboratory* 4: 237–250

- Tokioka, T. (1961). The structure of the operculum of the species of Atlantidae (Gastropoda: Heteropoda) as a taxonomic criterion, with records of some pelagic mollusks in the North Pacific. *Publications of the Seto Marine Biology Laboratory* 9: 267–332
- Tong, L.K.Y. (1988). The reproductive biology of *Thais clavigera* and *Morula musiva* (Gastropoda: Muricidae) in Hong Kong. *Asian Marine Biology* 5: 65–75
- Troschel, F.H. (& Thiele, J.) (1856–1893). *Das Gebiss der Schnecken, zur Begründung einer Natürlichen Classification*. Nicolaische Verlagsbuchhandlung : Berlin 2 vols, 252 pp., 409 pp. [Pts 1–6 (1856–1879); Pts 7 & 8 (1891–1893) by J. Thiele, written after Troschel's death]
- Trueman, E.R. (1968). The mechanism of burrowing of some naticid gastropods in comparison with that of other molluscs. *Journal of Experimental Biology* 48: 663–678
- Trueman, E.R. & Brown, A.C. (1992). The burrowing habit of marine gastropods. *Advances in Marine Biology* 28: 389–431
- Tsuchida, E. (1966). Taxonomic revision on two species of the genus *Oreotospira* (Gastropoda: Prosobranchia). *Venus* 45: 75–86
- Turner, R.D. (1948). The family Tonnidae in the Western Atlantic. *Johnsonia* 2: 165–192
- Turner, R.D. (1959). Notes on the genus *Taheitia* (Truncatellidae) in New Guinea with the description of a new species. *Occasional Papers on Mollusks, Harvard* 2(23): 181–188
- Tyler, A. (1939). Extraction of an egg membrane-lysin from sperm of the giant keyhole limpet (*Megathura crenulata*). *Proceedings of the National Academy of Sciences of the United States* 25: 317–323
- Tyler, A. (1940). Sperm agglutination in the keyhole limpet *Megathura crenulata*. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 78: 159–178
- Tyler, A. & Fox, S.W. (1940). Evidence for the protein nature of the sperm agglutinations of the keyhole limpet and sea urchin. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 79: 153–165
- Underwood, A.J. (1974). The reproductive cycles and geographical distribution of some common eastern Australian intertidal prosobranchs (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* 25: 63–88
- Underwood, A.J. (1975a). Comparative studies on the biology of *Nerita atramentosa* Reeve, *Bembicium nanum* (Lamarck) and *Cellana tramoserica* (Sowerby) (Gastropoda: Prosobranchia) in S.E. Australia. *Journal of Experimental Marine Biology and Ecology* 18: 153–172
- Underwood, A.J. (1975b). Intertidal zonation of prosobranch gastropods: analysis of densities of four co-existing species. *Journal of Experimental Marine Biology and Ecology* 19: 197–216
- Underwood, A.J. (1976a). Analysis of patterns of dispersion of intertidal prosobranch gastropods in relation to macroalgae and rockpools. *Oecologia (Heidelberg)* 25: 145–154
- Underwood, A.J. (1976b). Nearest neighbour analyses of spatial dispersion of intertidal prosobranch gastropods within two substrata. *Oecologia (Heidelberg)* 26: 257–266
- Underwood, A.J. (1976c). Food competition between age classes in the intertidal neritacean *Nerita atramentosa* (Gastropoda: Prosobranchia). *Journal of Experimental Marine Biology and Ecology* 23: 145–154
- Underwood, A.J. (1977). Movements of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology* 26: 191–201
- Underwood, A.J. (1978). An experiment evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia (Heidelberg)* 33: 185–202
- Underwood, A.J. (1979). The ecology of intertidal gastropods. *Advances in Marine Biology* 16: 111–210
- Underwood, A.J. (1981). Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology* 51: 57–85
- Underwood, A.J. (1984). Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia (Heidelberg)* 64: 211–222
- Underwood, A.J. & Chapman, M.G. (1989). Experimental analyses of the influence of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *Journal of Experimental Marine Biology and Ecology* 134: 175–196
- Underwood, A.J. & Chapman, M.G. (1992). Experiments on topographic influences on density and dispersion of *Littorina unifasciata* in New South Wales. Pp. 181–195 in Grahame, J., Mill, P.J. & Reid, D.G. (eds) *Proceedings of the Third International Symposium on Littorinid Biology*. Malacological Society of London : London
- Underwood, A.J. & Creese, R.G. (1976). Observations on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). II. The effects of available food on shell-banding patterns. *Journal of Experimental Marine Biology and Ecology* 23: 229–240
- Underwood, A.J. & McFadyen, K.E. (1983). Ecology of the intertidal snail *Littorina acutispira* Smith. *Journal of Experimental Marine Biology and Ecology* 66: 169–197
- Underwood, A.J. & Verstegen, P.H. (1988). Experiments on the association between the intertidal amphipod *Hyale media* Dana and the limpet *Cellana tramoserica* (Sowerby). *Journal of Experimental Marine Biology and Ecology* 119: 83–98
- Vahl, O. (1971). Growth and density of *Patina pellucida* (L.) (Gastropoda: Prosobranchia) on *Laminaria hyperborea* (Gunnerus) from Western Norway. *Ophelia* 9: 31–50
- Vail, V.A. (1977). Comparative reproductive anatomy of three viviparid gastropods. *Malacologia* 16: 519–540
- Valdez, M.F. & Briceno, J.A. (1980). Absorption of manganese by *Neritina latissima* (Gastropoda: Neritidae) in Costa Rica. *Revista de Biología Tropical* 28: 175–180
- Valentine, J.W. (1965). Quaternary Mollusca from Port Fairy, Victoria, Australia, and their palaeoecologic implications. *Proceedings of the Royal Society of Victoria* 78: 15–73
- Van Cleave, H.J. & Altringer, D.A. (1937). Studies on the life cycle of *Campeloma rufum*, a fresh-water snail. *American Naturalist* 71: 167–184
- van der Schalie, H. (1965). Observations on the sex of *Campeloma* (Gastropoda: Viviparidae). *Occasional Papers from the Museum of Zoology, University of Michigan* 641: 1–15
- Van Mol, J.-J. (1967). Etude morphologique et phylogénétique du ganglion cérébroïde des Gastéropodes Pulmonés (Mollusques). *Mémoires de l'Académie Royale de Belgique, Classes des Sciences* 37: 1–168
- Vaught, K. (1989). *A Classification of the Living Mollusca*. American Malacologists, Incorporated : Melbourne, Florida xii 195 pp. Edited by Abbott, R.T. & Boss, K.J.
- Vayssière, M.A. (1895). Etude sur l'organisation de l'*Homalogyra*. *Annales des Sciences Naturelles, Zoologie et Paléontologie* 19: 363–378
- Vayssière, A. (1923). Recherches zoologiques et anatomiques sur les mollusques de la famille des Cypræides. Part 1. *Annales du Musée d'Histoire Naturelle de Marseille* 18: 1–120
- Vayssière, A. (1927). Recherches zoologiques et anatomiques sur les mollusques de la famille des Cypræides. Part 2. *Annales du Musée d'Histoire Naturelle de Marseille* 22: 133–184
- Vella, P. (1953). The genus *Pellicaria* in the Tertiary of East Wairarapa. *Transactions of the Royal Society of New Zealand* 81: 35–48
- Verdonk, N.H. & Cather, J.N. (1983). Morphogenetic determination and differentiation. Pp. 215–252 in Verdonk, N.H., van den Biggelaar, J.A.M. & Tompa, A.S. (eds) *The Mollusca. Vol. 3. Development*. Academic Press : New York
- Vermeij, G.J. (1973). Morphological patterns in high intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* 20: 319–346
- Vermeij, G.J. (1978). *Biogeography and Adaptation: Patterns of Marine Life*. MA thesis, Harvard University, Cambridge
- Vermeij, G.J. (1979). Shell architecture and causes of death of Micronesian reef snails. *Evolution* 33: 686–696

15. PROSOBRANCHS

- Vermeij, G.J. (1981). Apertural form in gastropods. *Lethaia* 14: 104
- Vermeij, G. (1982). Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia* 23: 1–12
- Vermeij, G.J. & Zipser, E. (1986). Burrowing performance of some tropical Pacific gastropods. *The Veliger* 29: 200–206
- Vermeij, G.J., Zipser, E. & Dudley, E.C. (1980). Predation in time and space: peeling and drilling in terebrid gastropods. *Paleobiology* 6: 352–364
- Vermeulen, J.J. (1993). Notes on the non-marine molluscs of the island of Borneo 5. The genus *Diplommatina* (Gastropoda Prosobranchia: Diplommatinidae). *Basteria* 57: 3–69
- Verrill, A.E. (1880). Notice on the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science* (3) 20: 115–120
- Verrill, A.E. (1881a). Notice of recent additions of the marine invertebrates of the northeastern coast of America with descriptions of new genera and critical remarks on others. II. Mollusca with notes on Annelida, Echinodermata etc., collected by the US Fish Commission. *Proceedings of the United States National Museum* 3: 356–405
- Verrill, A.E. (1881b). Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, No. 2. *The American Journal of Science, Series 3* 22: 292–303
- Verrill, A.E. (1882). Catalogue of the marine Mollusca added to the fauna of New England during the last ten years. *Transactions of the Connecticut Academy of Sciences* 5: 447–599, pls 52–53
- Verrill, A.E. (1884). Second catalogue of Mollusca recently added to the fauna of New England coast and adjacent parts of the Atlantic, consisting mostly of deep sea species, with notes on other previously recorded. *Transactions of the Connecticut Academy of Sciences* 6: 139–294, pls 28–32
- Vestergaard, K. (1935). Über den Laich und die Larven von *Scalaria communis* (Lam.), *Nassarius pygmaeus* (Lam.) und *Bela turricula* (Mont.). *Zoologischer Anzeiger* 109: 217–222
- Villa, R. (1983). Note su habitat ed ecologia di *Addisonia lateralis* (Requien, 1848). *Notizario Centro Italiano Studi Malacologici* 5: 9–12
- Vincent, J.F.V. (1980). The hardness of the tooth of *Patella vulgata* L. radula: a reappraisal. *Journal of Molluscan Studies* 46: 129–133
- Vlès, F. (1907). Sur les ondes pédieuses des Mollusques reptateurs. *Compte Rendu Hebdomadaires des Séances de l'Académie des Sciences, Paris* 145: 276–278
- Vohra, F.C. (1965). Ecology of intertidal *Zostera* flats of Moreton Bay. Part 2. More detailed studies of a dominant animal, *Pyrasus ebeninus* (Brugière, 1792). PhD thesis, University of Queensland, Brisbane
- Vohra, F.C. (1970). Some studies on *Cerithidea cingulata* (Gmelin, 1791) on a Singapore sandy shore. *Proceedings of the Malacological Society of London* 39: 187–201
- Vokes, E.H. (1971). The geologic history of the Muricinae and Ocenebrinae. *Echo* 4: 37–54
- Vokes, E.H. (1974). Three species of Australian Muricidae (Gastropoda) with ancestors in the American Tertiary. *Journal of the Malacological Society of Australia* 3: 7–14
- Vokes, E.H. (1985). The genus *Dermomurex* (Mollusca: Gastropoda) in Australia. *Journal of The Malacological Society of Australia* 7: 45–65
- Vokes, E.H. (1993). Review of the muricine subgenus *Pterynotus* (*Pterochelus*) in Australia. *Journal of the Malacological Society of Australia* 14: 83–105
- Voltzow, J. (1983). Flow through and around the abalone *Haliotis kamtschatkana*. *The Veliger* 26: 18–21
- Voltzow, J. (1988). The organization of limpet pedal musculature and its evolutionary implications for the Gastropoda. Pp. 273–283 in Ponder, W.F. (ed.) *Prosobranch Phylogeny. Malacological Review, Supplement 4*
- Voltzow, J. (1994). Gastropoda: Prosobranchia. Pp. 111–252 in Harrison, F.W. & Kohn, A.J. (eds) *Microscopic Anatomy of Invertebrates. Vol. 5 Mollusca I*. Wiley-Liss: New York
- von Rohrback, F. (1937). Oekologische und morphologische Untersuchungen an *Viviparus* (*Bellamya*) *capillatus* Frauenfeld und *Viviparus* (*Bellamya*) *unicolor* Olivier, unter Berücksichtigung andere tropischer Formen und im Hinblick auf phyletische Beziehungen. *Archiv für Molluskenkunde* 69: 177–218
- Walker, C.G. (1968). Studies of the jaws, digestive system, and coelomic derivation in representatives of the genus *Acmaea*. *The Veliger, Supplement* 11: 88–97
- Walker, D.I., Kendrick, G.A. & McComb, A.J. (1988). The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. *Aquatic Botany* 30: 305–317
- Walker, D.I. & Prince, R.I.T. (1987). Distribution and biogeography of seagrass species on the north-west coast of Australia. *Aquatic Botany* 29: 19–32
- Wallace, C. (1978). Notes on the distribution of sex and shell characteristics in some Australian populations of *Potamopyrgus* (Gastropoda: Hydrobiidae). *Journal of the Malacological Society of Australia* 4: 71–76
- Wallace, C. (1979). Notes on the occurrence of males in populations of *Potamopyrgus jenkinsi*. *Journal of Molluscan Studies* 45: 61–67
- Wallace, C. (1985). On the distribution of the sexes of *Potamopyrgus jenkinsi* (Smith). *Journal of Molluscan Studies* 51: 290–296
- Walls, J.G. (1980). *Conchs, Tibias, and Harps*. T.F.H. Publications: Neptune, New Jersey 191 pp.
- Walne, P.R. (1956). The biology and distribution of the slipper limpet *Crepidula fornicata* in Essex rivers with notes on the distribution of the larger epi-benthic invertebrates. *Fishery Investigations (London)* (2) 20: 1–50
- Walsby, J. (1977). Population variations in the grazing turbinid *Lunella smaragda* (Mollusca: Gastropoda). *New Zealand Journal of Marine and Freshwater Research* 11: 211–238
- Walsby, J. & Morton, J.E. (1982). *Marine Molluscs, Cape Rodney to Okakari Point Marine Reserve. Pt 1. Chitons, limpets & topshells & pulmonates*. University of Auckland, Leigh Marine Laboratory: Auckland
- Warburton, K. (1973). Solar orientation in the snail *Nerita plicata* (Prosobranchia: Neritacea) on a beach near Watamu, Kenya. *Marine Biology* 23: 93–100
- Ward, J. (1965). The digestive tract and its relation to feeding habits in the stenoglossan prosobranch *Coralliophila abbreviata* (Lamarck). *Canadian Journal of Zoology* 43: 447–464
- Ward, J.E. & Langdon, C.J. (1986). Effects of the ectoparasite *Boonea* (*Odostomia*) *impressa* (Say) (Gastropoda: Pyramidellidae) on the growth rate, filtration rate, and valve movements of the host *Crassostrea virginica* (Gmelin). *Journal of Experimental Marine Biology and Ecology* 99: 163–180
- Ward, R.D. (1990). Biochemical genetic variation in the genus *Littorina* (Prosobranchia: Mollusca). *Hydrobiologia* 193: 53–69
- Warén, A. (1972). On the systematic position of *Fissurisepta granulosa* Jeffrey, 1882 and *Patella laterocompressa* de Rayneval & Ponzi, 1854 (Gastropoda, Prosobranchia). *Sarsia* 51: 17–24
- Warén, A. (1980a). Revision of the genera *Thyca*, *Stilifer*, *Scalenostoma*, *Mucronalia* and *Echineulima* (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* 9: 187–210
- Warén, A. (1980b). Descriptions of new taxa of Eulimidae (Mollusca, Prosobranchia), with notes on some previously described genera. *Zoologica Scripta* 9: 283–306
- Warén, A. (1981a). Eulimid gastropods parasitic on echinoderms in the New Zealand region. *New Zealand Journal of Zoology* 8: 313–324
- Warén, A. (1981b). Revision of the genera *Apicalia* A. Adams and *Stilapex* Iredale and description of two new genera (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* 10: 133–154
- Warén, A. (1983b). An anatomical description of *Eulima bilineata* Alder with remarks on and a revision of *Pyramidelloides* Nevill (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* 12: 273–294

- Warén, A. (1983a) A generic revision of the family Eulimidae (Gastropoda, Prosobranchia). *Journal of Molluscan Studies, Supplement* 13: 1–96
- Warén, A. (1989). New and little known Mollusca from Iceland. *Sarsia* 74: 1–28
- Warén, A. (1990). Ontogenetic changes in the trochoidean (Archaeogastropoda) radula, with some phylogenetic interpretations. *Zoologica Scripta* 19: 179–187
- Warén, A. (1991a). New and little known Mollusca from Iceland and Scandinavia. *Sarsia* 76: 53–124
- Warén, A. (1991b). New and little known 'skeneimorph' gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bollettino Malacologico* 27(10-12): 149–248
- Warén, A. (1993). New and little known Mollusca from Iceland and Scandinavia. Pt 2. *Sarsia* 78: 159–201
- Warén, A., Arnaud, P. M. & Cantera, J.R. (1986). Descriptions of two new gastropods of the Trichotropidae from Kerguelen and Crozet Islands (South Indian Ocean). *The Veliger* 29: 157–165
- Warén, A. & Bouchet, P. (1988). A new species of Vanikoridae from the western Mediterranean, with remarks on the northeast Atlantic species of the family. *Bollettino Malacologico* 24: 73–100
- Warén, A. & Bouchet, P. (1989). New gastropods from east Pacific hydrothermal vents. *Zoologica Scripta* 18: 67–102
- Warén, A. & Bouchet, P. (1990). Laubierinidae and Pisanianurinae (Ranellidae), two new deep-sea taxa of the Tonnoidea (Gastropoda: Prosobranchia). *The Veliger* 33: 56–102
- Warén, A. & Bouchet, P. (1991). Mollusca Gastropoda: Systematic position and revision of *Haloceras* Dall, 1889 (Caenogastropoda, Haloceratidae fam. nov.). *Mémoires du muséum National d'Histoire Naturelle, Zoologie* 150: 111–161
- Warén, A. & Bouchet, P. (1993). New records, species, genera, and a new family of gastropods from the hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22: 1–90
- Warén, A. & Gofas, S. (1996). *Kaiparapelta askewi* McLean & Harasewych, 1995 (Gastropoda: Pseudococculinidae): a spongirovous cocculiniform limpet and a case of remarkable convergence in radular morphology. *Haliotis* 25: 107–116
- Warén, A., Gofas, S. & Schander, C. (1993). Systematic position of three European heterobranch gastropods. *The Veliger* 36: 1–15
- Warén, A. & Hain, S. (1996). Description of Zeratulidae fam. nov. (Littorinoidea), with comments on an Antarctic littorinid gastropod. *The Veliger* 39: 277–334
- Warén, A. & Ponder, W.F. (1991). New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). *Zoologica Scripta* 20: 27–56
- Watson, D.C. & Norton, T.A. (1985). Dietary preferences of the common periwinkle *Littorina littorea* (L.). *Journal of Experimental Marine Biology and Ecology* 88: 193–211
- Weaver, C.S. & du Pont, J.E. (1970). *Living Volutes. A Monograph of the Recent Volutes of the World*. Delaware Museum of Natural History : Grenville 375 pp.
- Weber, H. (1924). Ein Umdreh- und Fluchtreflex bei *Nassa mutabilis*. *Zoologischer Anzeiger* 60: 261–269
- Weber, H. (1925). Über arhythmische Fortbewegung bei einigen Prosobranchiern. Ein Beitrag zur Bewegungsphysiologie der Gastropoden. *Zeitschrift für Vergleichende Physiologie* 2: 109–121
- Weber, H. (1927). Der Darm von *Dolium galea* L., eine vergleichend anatomischer Untersuchung unter besonderer Berücksichtigung der Tritonium-arten. *Zeitschrift für Morphologie und Ökologie der Tiere* 8: 663–804
- Wells, F.E. (1970). An ecological study of two sympatric species of *Fasciolaria* (Mollusca: Gastropoda) in Alligator Harbor, Florida. *The Veliger* 13: 95–108
- Wells, F.E. (1978). Zonation of marine gastropods on a rocky intertidal shore in the Admiralty Gulf, Western Australia, with emphasis on the genus *Nerita*. *The Veliger* 20: 279–287
- Wells, F.E. (1979). Ecological segregation among nerites at North-west Cape, Western Australia. *Journal of the Malacological Society of Australia* 4: 135–143
- Wells, F.E. (1980a). A comparative study of distributions of the mudwhelks *Terebralia sulcata* and *T. palustris* in a mangrove swamp in northwestern Australia. *Malacological Review* 13: 1–5
- Wells, F.E. (1980b). The distribution of shallow-water marine prosobranch gastropod molluscs along the coastline of Western Australia. *The Veliger* 22: 232–247
- Wells, F.E. (1984). Population characteristics of the periwinkle, *Nodilittorina unifasciata*, on a vertical rock cliff in Western Australia. *Nautilus* 98: 102–107
- Wells, F.E. (1985). The Potamididae (Mollusca: Gastropoda) of Hong Kong, with an examination of habitat segregation in a small mangrove system. Pp. 139–154 in Morton, B. & Dudgeon, D. (eds) *The Malacofauna of Hong Kong and Southern China 2. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 6-24 April 1983*. Hong Kong University Press : Hong Kong
- Wells, F.E. & Keesing, J.K. (1988). The limpet *Patelloida nigrosulcata* on intertidal platforms in the Perth area, Western Australia. *Journal of Molluscan Studies* 54: 53–57
- Wells, F.E. (1990). Revision of the recent Australian Turridae referred to the genera *Splendrillia* and *Austrodrillia*. *Journal of the Malacological Society of Australia* 11: 73–117
- Wells, F.E. (1991a). A new species of *Splendrillia*, with comments on two other species of the genus (Gastropoda: Turridae). *Journal of the Malacological Society of Australia* 12: 63–67
- Wells, F.E. (1991b). A revision of the Recent Australian species of the turrid genera *Clavus*, *Plagiostropha*, and *Tylotiella* (Mollusca: Gastropoda). *Journal of the Malacological Society of Australia* 12: 1–33
- Wells, F.E. (1994). A revision of the Recent Australian species of the turrid genera *Inquisitor* and *Ptychobela*. *Journal of the Malacological Society of Australia* 15: 71–102
- Wells, F.E. & Bryce, C.W. (1986). *Seashells of Western Australia*. Western Australian Museum : Perth 207 pp.
- Wells, F.E. & Bryce, C.W. (1988). *Seashells of Western Australia*. Western Australian Museum : Perth 2nd edn 207 pp.
- Wells, F.E. & Keesing, J.K. (1989). Reproduction and feeding in the abalone *Haliotis roei* Gray. *Australian Journal of Marine and Freshwater Research* 40: 187–197
- Wells, F.E. & Lalli, C.M. (1977). Reproduction and brood protection in the gastropods *Coralliophila abbreviata* and *C. caribaea*. *Journal of Molluscan Studies* 43: 79–87
- Wells, F.E. & Roberts, D. (1980). Molluscan assemblages on an intertidal sandflat in Princess Royal Harbour, Western Australia. *Australian Journal of Marine and Freshwater Research* 31: 499–507
- Wells, F.E. & Threlfall, T.J. (1981). Molluscs of the Peel Harvey estuarine system, with a comparison of other south-western estuaries. *Journal of the Malacological Society of Australia* 5: 101–111
- Wells, F.E. & Threlfall, T.J. (1982a). Reproductive strategies of *Hydrococcus brazieri* (Tenison Woods, 1876) and *Arthritica semen* (Menke, 1843) in Peel Inlet, Western Australia. *Journal of the Malacological Society of Australia* 5: 157–166
- Wells, F.E. & Threlfall, T.J. (1982b). Salinity and temperature tolerance of *Hydrococcus brazieri* (T. Woods, 1876) and *Arthritica semen* (Menke, 1843) from the Peel-Harvey estuarine system, Western Australia. *Journal of the Malacological Society of Australia* 5: 151–156
- Wells, H.W. (1958). Feeding habits of *Murex fulvescens*. *Ecology* 39: 556–558
- Welsch, U. & Storch, V. (1969). Über das Osphradium der prosobranchen Schnecken *Buccinum undatum* und *Neptunea antiqua*. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 95: 317–330
- Wenz, W. (1938–1944). Gastropoda. Teil 1, Allgemeiner Teil [pp. 1–84] und Prosobranchia [pp. 85–231]. In Schindewolf, O.H. (ed.) *Handbuch der Paläozoologie. Vol. 6. Gebrüder Bornträger* : Berlin vi 1639 pp.

15. PROSOBRANCHS

- Werner, B. (1952). Ausbildungsstufen der Filtrationsmechanismen bei filtrierenden Prosobranchiern. *Verhandlungen der Deutschen Zoologischen Gesellschaft 1951, Zoologischer Anzeiger, Supplement* 17: 529–546
- Werner, B. (1953). Über der Nahrungserwerb der Calyptraeidae (Gastropoda: Prosobranchia). Morphologie, Histologie und Funktion der am Nahrungserwerb beteiligten Organe. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 4: 260–315
- Werner, B. (1955). Über die Anatomie, Entwicklung und Biologie des Veligers und der Veliconcha von *Crepidula fornicata* L. (Gastropoda Prosobranchia). *Helgoländer Wissenschaften Meeresuntersuchungen* 5: 169–217
- Werner, B. (1959). Das Prinzip des endlosen Schleimfilters beim Nahrungserwerb wirbellosen Meerestiere. *International Revue der Gesamten Hydrobiologie und Hydrographie* 44: 181–216
- West, D.L. (1973). Notes on the development of *Colus stimpsoni*. *The Nautilus* 87: 1–4
- West, D.L. (1978a). Reproductive biology of *Colus stimpsoni*. 1. Male genital system. *The Veliger* 20: 266–273
- West, D.L. (1978b). Reproductive biology of *Colus stimpsoni*. 2. Spermiogenesis. *The Veliger* 21: 1–9
- West, D.L. (1978c). Reproductive biology of *Colus stimpsoni*. 3. Female genital system. *The Veliger* 21: 432–438
- West, D.L. (1979). Reproductive biology of *Colus stimpsoni* (Prosobranchia: Buccinidae). III. Female genital system. *The Veliger* 21: 432–438
- West, T.L. (1990). Feeding behaviour and functional morphology of the epiproboscis of *Mitra edae* (Mollusca: Gastropoda; Mitridae). *Bulletin of Marine Science* 46: 761–779
- West, T.L. (1991). Functional morphology of the proboscis of *Mitra catalinae* Dall, 1920 (Mollusca: Gastropoda: Mitridae), and the evolution of the mitrid epiproboscis. *Bulletin of Marine Science* 48: 702–718
- Whitaker, M.B. (1951). On the homologies of the oesophageal glands of *Theodoxus fluviatilis* (L.). *Proceedings of the Malacological Society of London* 29: 21–34
- Wigham, G.D. (1975). Environmental influences upon the expression of shell form in *Rissoa parva* (Da Costa). *Journal of the Marine Biological Association of the United Kingdom* 55: 425–438
- Wigham, G.D. (1976). Feeding and digestion in the marine prosobranch *Rissoa parva* (da Costa). *Journal of Molluscan Studies* 42: 74–94
- Williams, W.D. & Mellor, M.W. (1991). Ecology of *Coxiella* (Mollusca, Gastropoda, Prosobranchia), a snail endemic to Australian salt lakes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 84: 339–355
- Wilson, B.R. (1969). Use of the propodium as a swimming organ in an ancillia (Gastropoda: Olividae). *The Veliger* 11: 340–342
- Wilson, B.R. (1972). New species and records of Volutidae (Gastropoda) from Western Australia. *Journal of the Malacological Society of Australia* 2: 229–360
- Wilson, B.R. (1985). Direct development in southern Australia cowries (Gastropoda: Cypraeidae). *Australian Journal of Marine and Freshwater Research* 36: 267–280
- Wilson, B.R. (1993). *Australian Marine Shells. Part 1. Prosobranch Gastropods*. Odyssey Publishing : Kallaroo, Western Australia 408 pp.
- Wilson, B.R. (1994). *Australian Marine Shells. Prosobranch Gastropods Pt 2 (Neogastropods)*. Odyssey Publishing : Kallaroo, Western Australia 370 pp.
- Wilson, B.R. & Gillett, K. (1971). *Australian Shells*. A.H. & A.W. Reed Books : Sydney 168 pp.
- Wilson, B.R. & Gillett, K. (1979). *A Field Guide to Australian Shells. Prosobranch Gastropods*. Reed Books : Sydney 287 pp.
- Wilson, B.R. & Gillett, K. (1988). *A Field Guide to Australian Shells. Prosobranch Gastropods*. Reed Books : Sydney reprint 287 pp.
- Wilson, B.R. & McComb, J.A. (1967). The genus *Cypraea* (subgenus *Zoila* Jousseaume). *Indo-Pacific Mollusca* 1: 457–488
- Wilson, B.R. & Summers, R. (1966). Variation in the *Zoila friendi* (Gray) species complex (Gastropoda: Cypraeidae) in south-western Australia. *Journal of the Malacological Society of Australia* 1(9): 3–24
- Wingstrand, K.G. (1985). On the anatomy and relationships of Recent Monoplacophora. *Galathea Report* 16: 7–94
- Wise, J.B. (1993). Anatomy and functional morphology of the feeding structures of the ectoparasitic gastropod *Boonea impressa* (Pyramidellidae). *Malacologica* 55: 119–134
- Wise, J.B. (1996). Morphology and phylogenetic relationships of certain pyramidellid taxa (Heterobranchia). *Malacologia* 37: 443–511
- Wolff, T. (1976). Utilization of seagrass in the deep sea. *Aquatic Botany* 2: 161–174
- Wolff, T. (1979). Macrofaunal utilization of plant remains in the deep-sea. *Sarsia* 64: 117–136
- Work, R.C. (1969). Systematics, ecology and distribution of the molluscs of Los Roques, Venezuela. *Bulletin of Marine Science* 19: 614–711
- Worthington, D.G. & Fairweather, P.G. (1989). Shelter and food: interactions between *Turbo undulatum* (Archaeogastropoda: Turbinidae) and coralline algae on rocky seashores in New South Wales. *Journal of Experimental Marine Biology and Ecology* 129: 61–79
- Wright, W.G. & Lindberg, D.R. (1982). Direct observation of sex change in the patellacean limpet *Lottia gigantea*. *Journal of the Marine Biological Association of the United Kingdom* 62: 737–738
- Wu, S.-K. (1965). Comparative functional studies on the digestive system of the muricid gastropods *Drupa ricina* and *Morula granulata*. *Malacologia* 3: 211–233
- Yamada, S.B. (1982). Growth and longevity of the mud snail *Batillaria atramentaria*. *Marine Biology* 67: 187–192
- Yamaguchi, M. (1977). Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Marianas Islands. *Marine Biology* 44: 249–263
- Yipp, M.W. (1980). The functional morphology of the organs of feeding and digestion in *Crepidula walshi* (Prosobranchia: Calyptraeidae). Pp. 221–252 in Morton, B. (ed.) *The Malacofauna of Hong Kong and Southern China. Proceedings of the First International Workshop on the Malacofauna of Hong Kong and Southern China, 1980*. Hong Kong University Press : Hong Kong
- Yipp, M.W. (1993). An analysis of heat and desiccation stresses as critical environmental factors on a rocky shore. Pp. 621–631 in Wells, F.E. (ed.) *The Marine Flora and Fauna of Rottnest Island, Western Australia, Vol. 2. Fifth International Marine Biological Workshop, Rottnest Island, Western Australia, 1991*. Western Australian Museum : Perth
- Yochelson, E.L. (1984). Historic and current considerations for revision of Paleozoic gastropod classification. *Journal of Paleontology* 58: 259–269
- Yochelson, E.L. (1988). A new genus of Patellacea (Gastropoda) from the Middle Ordovician of Utah: The oldest known example of the superfamily. *New Mexico Bureau of Mines and Mineral Resources, Memoir* 44: 195–200
- Yonge, C.M. (1932). Notes on feeding and digestion in *Pterocera* and *Vermetus* with a discussion of the occurrence of the crystalline style in the Gastropoda. *Scientific Reports of the Great Barrier Reef Expedition 1928–29* 1: 259–281
- Yonge, C.M. (1938). Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus*. *Journal of the Marine Biological Association of the United Kingdom* 22: 453–468
- Yonge, C.M. (1946). On the habits of *Turritella communis* Risso. *Journal of the Marine Biological Association of the United Kingdom* 26: 377–380
- Yonge, C.M. (1947). The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London, Series B* 232: 443–518
- Yonge, C.M. (1953). Observations on *Hipponix antiquatus* (Linnaeus). *Proceedings of the California Academy of Sciences* 28: 1–24

- Yonge, C.M. (1960a). Further observations on *Hipponix antiquatus* with notes on North Pacific pulmonate limpets. *Proceedings of the California Academy of Sciences, Fourth Series* 31: 111–119
- Yonge, C.M. (1960b). Mantle cavity, habits and habitat in the blind limpet *Lepeta concentrica* Middendorff. *Proceedings of the Californian Academy of Sciences* 31: 103–110
- Yonge, C.M. (1962). On the biology of the mesogastropod *Trichotropis cancellata* Hinds, a benthic indicator species. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 122: 160–181
- Yoo, E.K. (1994). Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. *Records of the Australian Museum* 46: 63–120
- Zeigler, R.F. & Porreca, H.C. (1969). *Olive Shells of the World*. Zeigler & Porreca : New York 96 pp.
- Ziegelmeier, E. (1954). Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda: Prosobranchia). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 5: 1–33
- Ziegelmeier, E. (1958). Zur Lokomotion bei Naticiden (Gastropoda, Prosobranchia). (Kurze Mitteilung über aushwimbewegungen bei *Polynices josephinus* Risso.) *Helgoländer Wissenschaftliche Meeresuntersuchungen* 6: 202–206
- Ziegelmeier, E. (1961). Zur Fortpflanzungsbiologie der Naticiden (Gastropoda: Prosobranchia) (Laichringo und Laichakt bei *Lunatia nitida* Donovan). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 8: 94–118
- Zilch, A. (1959–1960). Gastropoda, Teil 2, Euthyneura. In Schindewolf O.H. (ed.) *Handbuch der Paläozoologie*. Vol. 6. Gebrüder Bornträger : Berlin xii 834 pp.
- Zinsmeister, W.J. (1982). Late Cretaceous-early Tertiary molluscan biogeography of the southern circum-Pacific. *Journal of Paleontology* 56: 84–102
- Zinsmeister, W.J. & Camacho, H.H. (1980). Late Eocene Struthiolariidae (Mollusca: Gastropoda) from Seymour Island, Antarctic Peninsula and their significance to the biogeography of early Tertiary shallow-water faunas of the Southern Hemisphere. *Journal of Paleontology* 54: 1–14

OPISTHOBRANCHIA

CHAPTER 16

DEFINITION AND GENERAL DESCRIPTION

Opisthobranchs, often known collectively as 'sea slugs', include the most colourful and structurally diversified Gastropoda. All grades of body organisation are expressed in adult animals from fully shelled to completely shell-less (Figs 16.1, 16.2). Evolutionary trends such as reduction and loss of the shell have often occurred in parallel in independent lineages, and successive stages are recognisable in living taxa.

The most primitive opisthobranchs are small sand-dwellers that have a heterostrophic larval shell (protoconch), and a dextrally coiled adult shell (teleoconch) with elevated spire and sculpture of punctate spiral grooves. The animal can retract completely into its shell, which is then closed, albeit imperfectly, by an operculum. Such primitive opisthobranchs underwent early reduction of the shell (associated with a move to hard substrata) by way of

decreased calcification, whorl shortening and apertural enlargement and the loss of the operculum. Ultimately the shell, sunk beneath the integument, was reduced to an internal plate, and even that was finally lost.

At the same time as the shell was being reduced, the opisthobranch body was extensively reorganised. The mantle cavity, so important for the antecedent prosobranchs, was displaced posteriorly (Brace 1977a) and became shallower. Eventually the mantle cavity was lost altogether, along with its associated osphradium and hypobranchial gland. The dorsal mantle lobe spread to form a roof over the body. The anus migrated from the mantle cavity along the right side to a mid-dorsal position. Novel respiratory structures like ciliated ridges (raphes), the aplysiid plicate gill, the pleurobranch bipinnate gill, the circular mid-dorsal dorid gill and cerata evolved independently in larger forms, while smaller forms relied on simple integumentary respiration (Morton 1972).

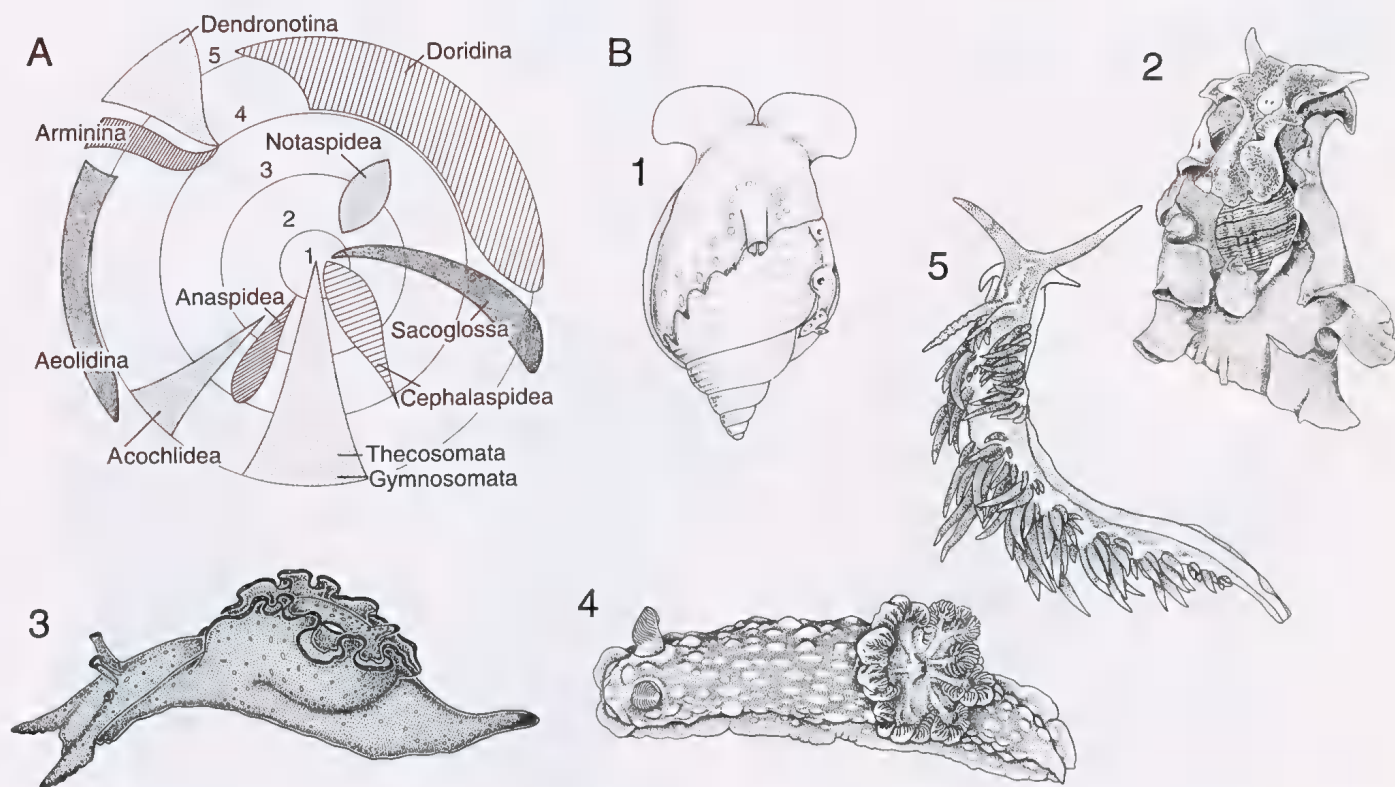


Figure 16.1 A, a broad characterisation of grades of organisation in the Opisthobranchia: **Grade 1**, early level with fully spiral shell, sometimes with an operculum, mantle cavity unmodified and nerve loop streptoneurous (for example, *Acteon*, *Bullina*, *Ringicula*, *Cylindrobulla*); **Grade 2**, coiled shell and mantle cavity diminished in importance, with great enlargement of foot and head shield, and operculum lost (for example, *Haminoea*, *Hydatina*); **Grade 3**, a slug-like form with further reduction of the shell to a small internal plate, mantle cavity strongly reduced or lost, but single gill persists (for example, *Philine*, *Aplysia*, *Berthella*, *Phanerophthalmus*); **Grade 4**, a bilaterally symmetrical 'nudibranch', with complete loss of shell and substitution of a dorsal mantle, placement of rhinophores anteriorly and anus postero-medially, and with a branchial cirlet (for example, *Archidoris*, *Chromodoris*); **Grade 5**, dorsal outgrowths (cerata) dominate the external symmetry with the eventual display of the gland outside the dorsum, and gills circumanal, sometimes dendritic tufts, or respiratory cerata (for example, *Tritonia*, *Marianina*, *Janolus*, *Phidiana*, *Okenia*). B, An example of an animal from each grade: 1, *Ringicula* sp. (Cephalaspidea); 2, *Hydatina physis* (Cephalaspidea); 3, *Aplysia parvula* (Anaspidea); 4, *Gymnodoris plebeia* (Doridoidea); 5, *Phidiana newcombi* (Aeolidioidea). (A, after Willan & Morton 1984)

[A, C. Eadie; B: 1, 2, R. Plant; 3, L. Newman; 4, 5, S. Weidland]

16. OPISTHOBANCHIA

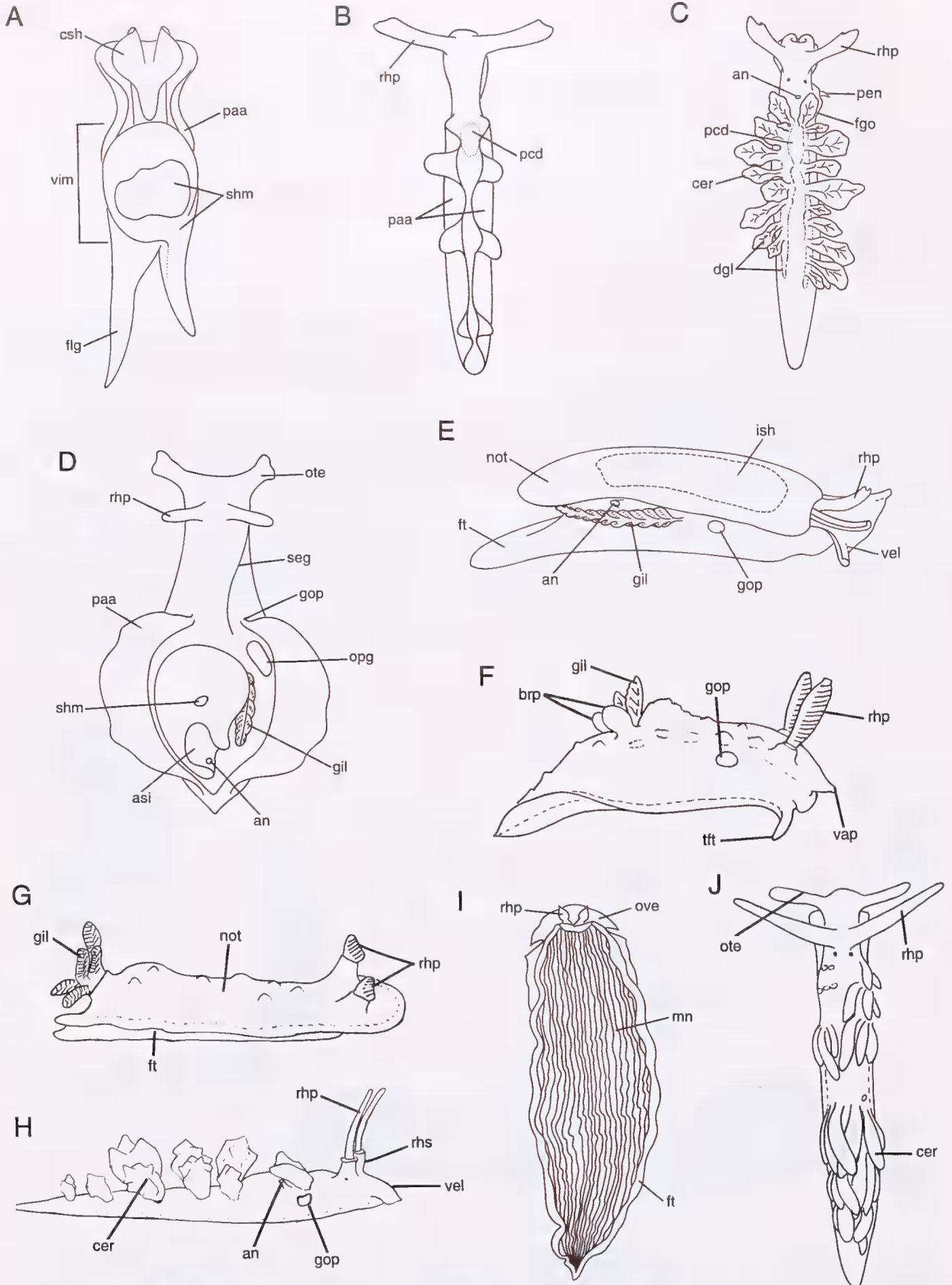


Figure 16.2. External features of the Opisthobranchia. A, order Cephalaspidea, *Noalda*. B, C, order Sacoglossa: B, *Elysia*; C, *Hermaea*. D, order Anaspidea, *Aplysia*. E, order Notaspidea, *Berthella*. F–J, order Nudibranchia: F, suborder Doridina, superfamily Anadoridoidea, *Polycera*; G, suborder Doridina, superfamily Eudoridoidea, *Aphelodoris*; H, suborder Dendrotina, *Doto*; I, suborder Arminina, *Armina*; J, suborder Aeolidina. an, anus; asi, anal siphon; brp, branchial appendages; cer, cerata; csh, cephalic shield; dgl, digestive gland; fgo, female genital opening; flg, flagellum; ft, foot; gil, gill(s); gop, genital aperture; ish, internal shell; mn, mantle; not, notum; opg, opaline gland; ote, oral tentacle; ove, oral veil; paa, parapodium; pcd, pericardium; pen, penis; rhp, rhinophore(s); rhs, rhinophore sheath; seg, seminal groove; shm, shell enclosed by mantle; tft, tentaculiform foot corner; vap, velar appendage; vel, velum; vim, visceral mass. (After Burn 1989)

[C. Eadie]

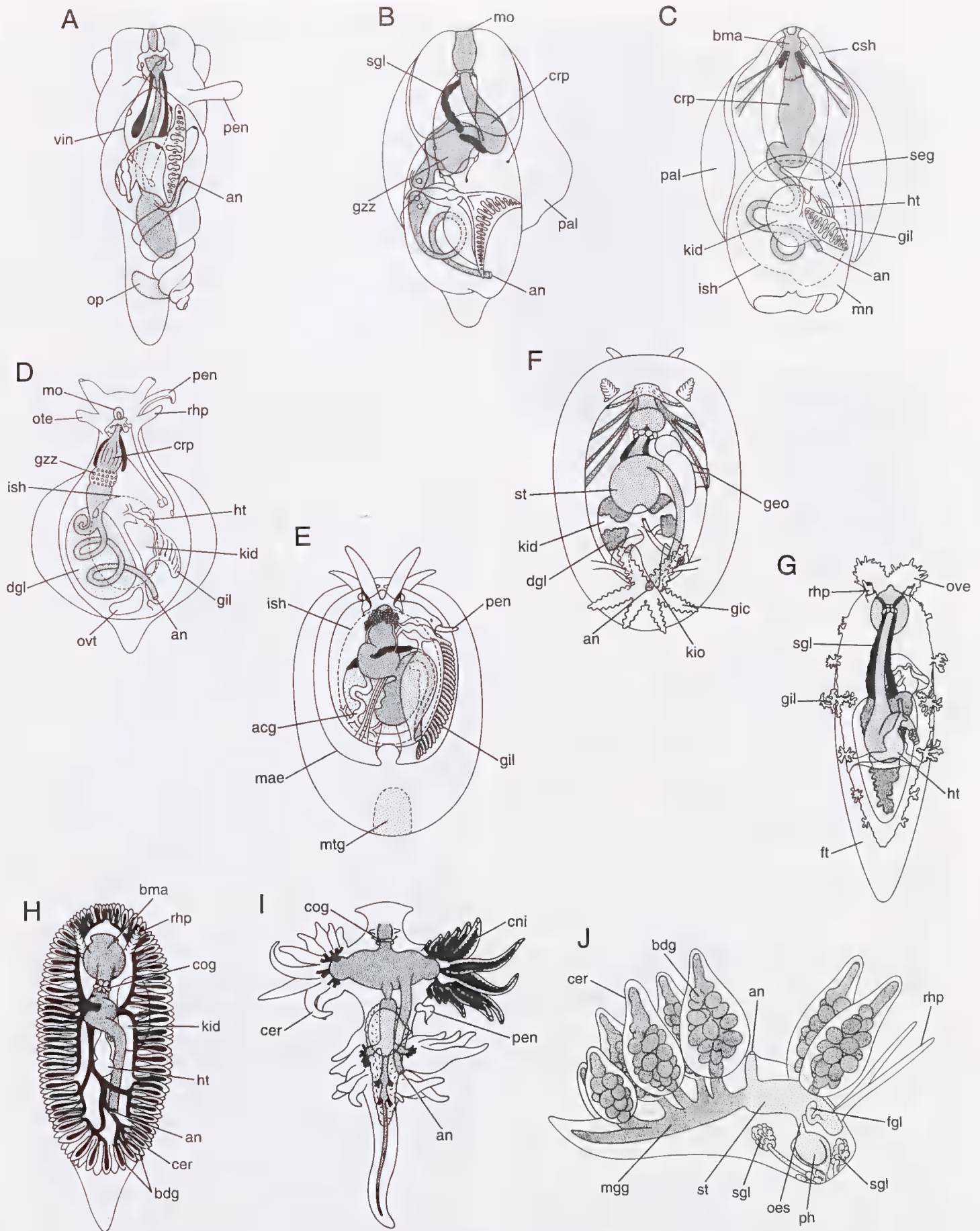


Figure 16.3 Internal anatomy of representative Opisthobranchia shown diagrammatically in dorsal view (A–I) and lateral view (J). A–C, order Cephalaspidæ: A, *Acteon*; B, *Haminoea*; C, *Philine*. D, order Anaspidea, *Aplysia*. E, order Notaspidea, *Pleurobranchus*. F–J, order Nudibranchia: F, suborder Doridina; G, suborder Dendronotina; H, suborder Arminina; I, suborder Aeolidina; J, suborder Aeolidina, *Embletonia*, showing the dorsal cerata filled with branches of the digestive gland. acg, acid gland duct; an, anus; bdg, branches of digestive gland; bma, buccal mass; cer, cerata; cni, cnidosacs; cog, circumoesophageal nerve ring; crp, crop; csh, cephalic shield; dgl, digestive gland; fgl, foregut gland; ft, foot; geo, genital openings; gic, gill circlet; gil, gill(s); gzz, gizzard; ht, heart; ish, internal shell; kid, kidney; kio, kidney opening; mae, mantle edge; mgg, midgut gland; mn, mantle; mo, mouth; mtg, metapodial mucous gland; oes, oesophagus; op, operculum; ote, oral tentacle; ove, oral veil; ovt, ovotestis; pal, parapodial lobe(s); pen, penis; ph, pharynx; rhp, rhinophore(s); seg, seminal groove; spl, salivary gland; st, stomach; vin, visceral nerve cords. (A–I, after Thompson 1988; J, after Hyman 1967) [A–I, C. Eadie; J, I. Hallam]

16. OPISTHOBRANCHIA

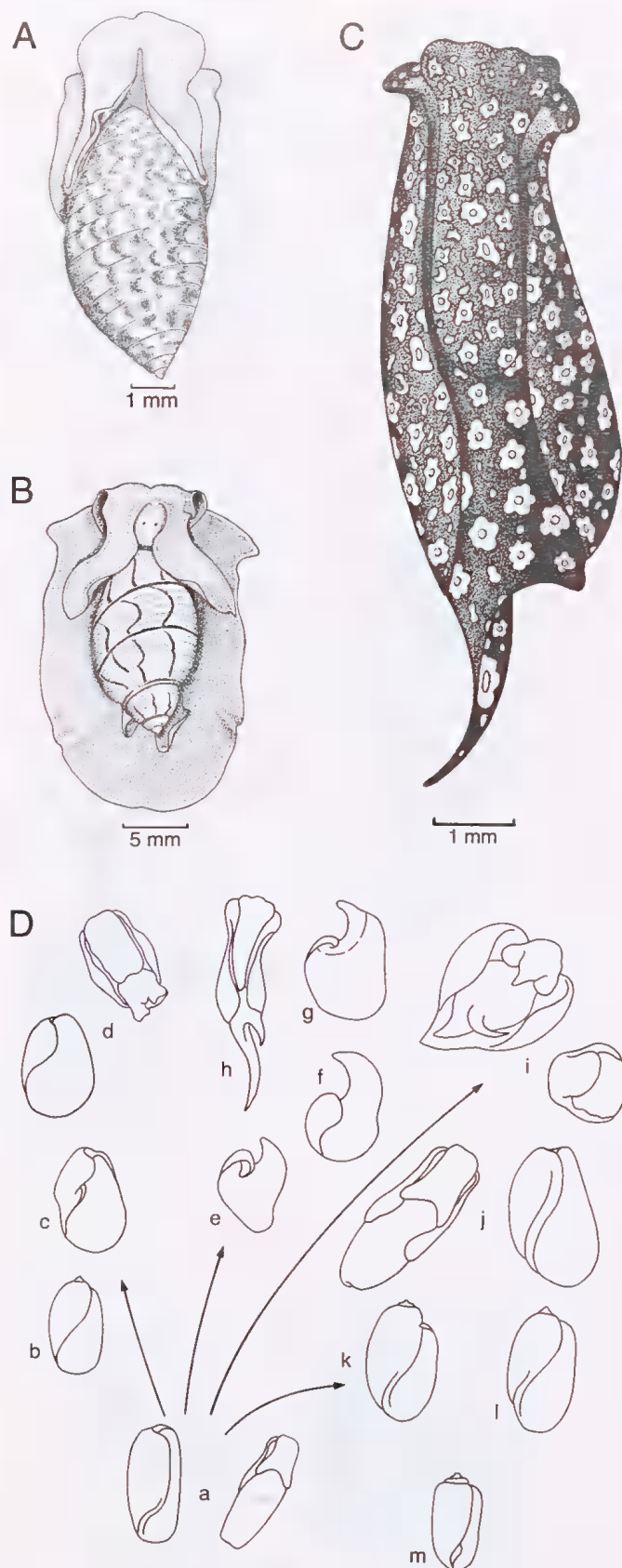


Figure 16.4 A–C, evolutionary trends in cephalaspidean body form from a 'snail' in which the shell dominates the shape of the body, to a 'slug' in which the shell is either absent or reduced to an internal remnant. A, *Pupa sulcata* (Acteonidae). B, *Bullina lineata* (Bullinidae). C, *Chelidonura sandrana* (Aglajidae). D, reduction of the shell has occurred, independently, in many lineages in the Philinoidea: a, Cylichnidae, *Cylichna alba*, animal and shell; b–d, Philinidae – b, *Philine lima*; c, *Philine umbilicata*; d, *Philine angasi*, animal and shell; e–h, Aglajidae – e, *Melanochlamys cylindrica*; f, *Odontoglossa guamensis*; g, *Philinopsis taronga*; h, *Chelidonura* sp.; i, Gastropteridae, *Gastropteron bicornutum*, animal and shell; j–m, Scaphandridae – j, *Scaphander lignarius*, animal and shell; k, *Paracteocina viijazi*; l, *Meloscaphander grandis*; m, *Tornatina candei*. (A, after Rudman 1972a; B, after Rudman 1972b; C, after Rudman 1973; E, after Rudman 1978) [A–C, T.E. Thompson; D, D. Wahl]

Loss of the shell has allowed opisthobranchs to depart further than any other gastropod group from the ancestral gastropod form. The head, foot and mantle have become elaborated in diverse ways. Most remarkable has been the evolution of repugnatory glands to take on the role of bodily protection by chemical rather than physical means. Such chemical defences are often reinforced by aposematic colouration.

The foot of opisthobranchs is generally like that of the antecedent gastropods. Smaller forms creep using cilia and mucus, whereas more bulky forms crawl by muscular waves. In several lineages the foot is expanded laterally to form wing-like outgrowths (parapodia) that are usually adaptations for sustained swimming.

Primitively the head is surmounted by a cephalic shield with specialised lateral sensory areas (Hancock's organ). Although this shield suffered shortening with the ancestors' move from surface deposits, its posterior corners became elaborated to form novel chemosensory tentacles, the rhinophores.

The mouth is often surrounded by a pair of oral tentacles. During feeding the pharynx is protruded directly onto the food. This muscular pharynx contains two jaws and a radula. Primitively the radula contains numerous rows of teeth, but in advanced forms it is reduced to just a single row. Composite oral and/or tubular salivary glands are present. The oesophagus is sometimes partitioned into a thin-walled crop and muscular gizzard with cuticularised masticatory plates. The simple stomach is associated with the digestive gland which can be either a solid mass (holohepatic) or ramified throughout the body (cladohepatic). The ultimate diverticula of the digestive gland end near the body surface or penetrate integumentary structures such as cerata. The intestine and rectum are relatively short. The anus is placed well behind the head. Even in those opisthobranchs with deep mantle cavities, the anus opens much further back than in most caenogastropods.

The heart complex is located within a pericardium, and it generally consists of a single ventricle and auricle. One or two renopericardial ducts may unite the pericardium with the often sac-like kidney.

The central nervous system in primitive forms is streptoneurous or chiasmoneurous, with crossing of the cerebrovisceral connectives and supra-intestinal ganglion on the left and sub-intestinal ganglion on the ventral right. It is mostly secondarily euthyneurous in advanced forms, with an uncrossed visceral loop and increased cephalisation and cerebralisation. Statocysts are present. The eyes are frequently reduced and embedded in the integument; they are never stalked or extensible as in stylomatophoran pulmonates.

The reproductive system is hermaphroditic. In the female system, the pallial oviduct has a proximal seminal receptacle for long-term storage of foreign (exogenous) sperm, a cluster of nidamental glands (separate albumen, mucous and membrane glands), and a distal bursa copulatrix for the reception of sperm during copulation and gametolysis after fertilisation. The male system commences with an ampulla, an enlargement of the coelomic gonoduct, for storage of its own sperm. The male pallial gonoduct consists of vas deferens, prostate gland and penis. Primitively the penis is a projection on the side of the head and this is connected to a common genital opening by an open, ciliated seminal groove (monaulic condition). In advanced opisthobranchs, the penis is protrusible and located on the right side of the body immediately in front of the female gonopore. The pallial gonoduct may be split into two (diaulic) or three ducts (triaulic, with separate channels for endogenous sperm, exogenous sperm and eggs) (Ghiselin 1966). Fertilisation is internal in all opisthobranchs that have been studied. Eggs are laid in encapsulated, gelatinous masses. Primitively, most opisthobranchs have free-swimming, planktotrophic larvae.

Opisthobranchs are almost exclusively marine, the only exceptions being some freshwater acochlidians. As a group, opisthobranchs have undergone major evolutionary radiations in connection with habitat and diet, but none is parasitic. Species are known from almost every marine habitat; some are planktonic.

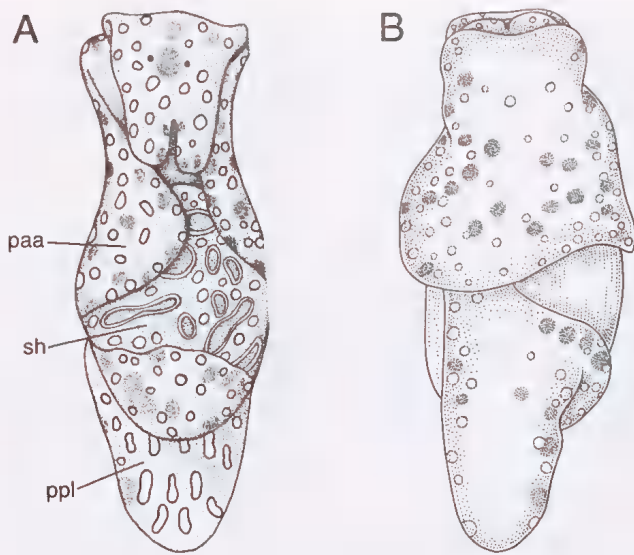


Figure 16.5 *Haminoea cymbalum* (Haminoeidae) showing the posterior pallial lobe of the 'foot' which is an extension of the mantle: A, dorsal view; B, ventral view. paa, parapodia; ppl, posterior pallial lobe; sh, shell. (After Rudman 1971a) [A, T.E. Thompson; B, R. Plant]

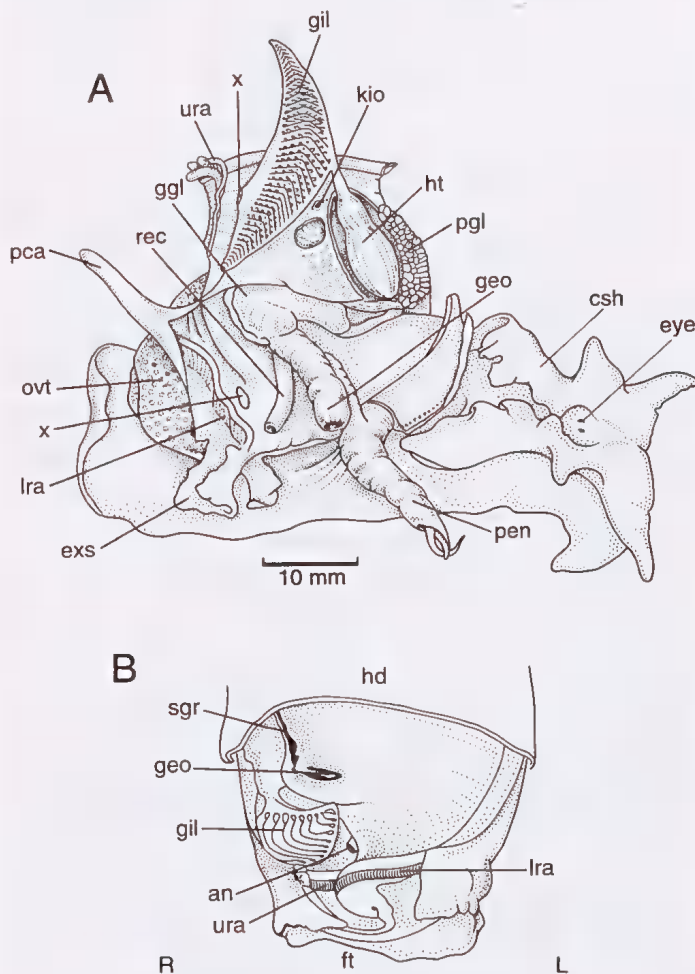


Figure 16.6 Change in the body shape of opisthobranchs during detorsion and loss of the mantle cavity. A, mantle cavity (viewed from right) of *Hydatina physis* (Hydatinidae), a typical, primitive cephalaspidean, showing the position of attachment of the gill to the mantle cavity floor. B, *Melanochlamys* sp. (Aglajidae), ventral view of mantle cavity with posterior foot removed, illustrating the shift of the mantle cavity and associated openings to the right of the body. an, anus; csh, cephalic shield; exs, exhalant siphon; eye, eye; ft, foot; geo, genital opening; ggl, genital gland; gill, gill; hd, head; ht, heart; kio, kidney opening; L, left; lra, lower raphe; ovt, ovotestis; pca, pallial caecum; pen, penis; pgl, pericardial gland; R, right; rec, rectum; sgr, seminal groove; ura, upper raphe; x, point of attachment of gill to mantle cavity floor. (A, after Rudman 1972a; B, Rudman 1971a) [R. Plant]

HISTORY OF DISCOVERY

The history of discovery of opisthobranchs in Australia is best considered separately for those with shells and those without. Shelled species in the orders Cephalaspidea, Sacoglossa, Anaspidea and Notaspidea were not distinguished from caenogastropods or other shelled molluscs by early collectors and so their discovery follows the path described elsewhere for other marine shells.

The difficulty of finding a method that preserved shell-less opisthobranchs in a condition similar to that in life meant that the growth in our knowledge of the Australian fauna was slower, and is still more incomplete, than that of most shell-bearing molluscs. Since specimens often become distorted and lose colour on preservation, the determination of the name of a sea slug requires an accurate record of the external shape and an indication of the colour of the living animal, usually by a drawing. Such time-consuming tasks were generally beyond the capacity of collectors on the early voyages.

Australian collections were first made during the French expedition of *Le Géographe* and *Le Naturaliste* under the command of Nicolas Baudin with the naturalist Péron on board, between 1801 and 1803. The expedition visited Shark Bay, Western Australia, in June/July 1801 and again in March 1803. On one of these visits the first known nudibranch from Australia was collected. Later it was named *Doris maculosa* by Cuvier (1804). The short original description and poor state of preservation of the specimen, still in the collection of the National Museum of Natural History, Paris, make the identification of this species virtually impossible. Some anatomical details from a later study (Pruvot-Fol 1935), suggest the species may belong to the genus *Discodoris*. The material collected on this expedition well illustrates the problems surrounding such early collections. Other species of nudibranchs were collected, some from Timor and some from Ile de France (Mauritius). The absence of any information on colour makes identification of all these species very difficult. The locality data may also be suspect, for one species purportedly collected at Timor, *Doris pustulosa*, is possibly *Ceratosoma brevicaudatum*, a species found only in southern Australian waters (Rudman 1988).

Nudibranchs were next recorded by another French expedition led by Dumont d'Urville in *l'Astrolabe*. The famous naturalists Jean Quoy and Joseph Gaimard collected the cephalaspideans *Adamnestia arachis* and *Liloea brevis* from King George Sound, Western Australia, and the notaspidean *Berthella punctata* (Quoy & Gaimard 1832) and the nudibranchs *Dendrodoris violacea* and *D. aurea* from Jervis Bay, New South Wales. The common sacoglossan *Elysia australis* was found on shores near Sydney. Some of this material still exists, although in poor condition, in Paris, and good colour illustrations of many of the specimens were painted. Some of these were published in the expedition reports and others are retained in the archives of the National Museum of Natural History, Paris.

A series of expeditions from Port Jackson (Sydney) to survey the Australian coast began early in the 19th century, for example, the *Mermaid* (P.P. King, 1815–1820), the *Bathurst* (1821–1822) and HMS *Herald* (Denham, 1852–1855). Most famous were the surveys of the Queensland coast by HMS *Fly* (1842–1845) and HMS *Rattlesnake* (1846–1849). All these voyages carried active naturalists or officers with an interest, or expertise, in natural history, including Cunningham, Ince, Jukes, Huxley and MacGillivray. Much of the material collected was sent to England where, either directly or indirectly, it ended up in the collections of the British Museum. Regrettably, no information was recorded on the living shape or colour and the species described from these collections – *Ceratosoma brevicaudatum*, *C. oblongum*, *Sphaerodoris incii*, *Asteronotus cruenta* (Gray 1850), *Plocamopherus naevatus*, *Doris analampulla*, *D. collatata*, *D. peculiaris*, *D. praetenera*, *D. pustulata* and *Doriopsis australiensis* (Abraham 1876, 1877). With two exceptions (*C. brevicaudatum* and *D. peculiaris*), these are probably unidentifiable.

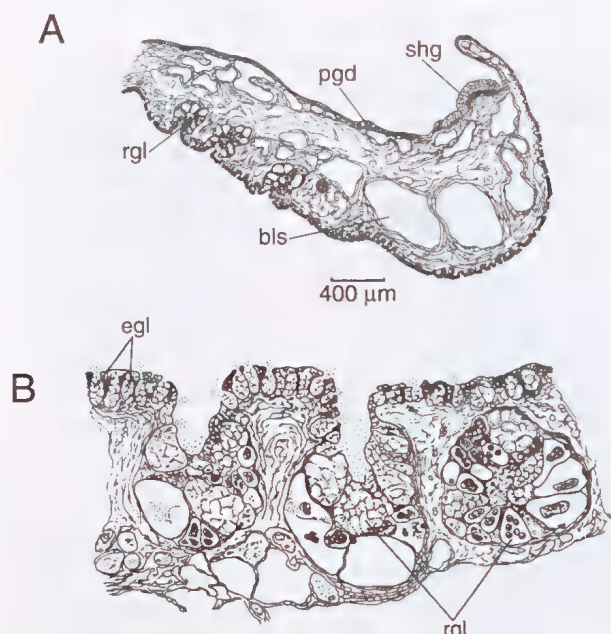


Figure 16.7 Sections through the mantle roof showing the epidermal glands which are considered to be defensive. **A**, the edge of the mantle roof of *Hydatina physis* (Hydatinidae), showing the location of the repugnatorial glands which produce a white acidic secretion. **B**, the large compound repugnatorial glands and small epithelial secretory cells of *Pupa kirki* (Acteonidae). bls, blood sinus; egl, small epithelial secretory glands; pgd, pigment gland; rgl, repugnatorial gland; shg, shell gland. (A, after Rudman 1972a; B, after Rudman 1972b) [R. Plant]

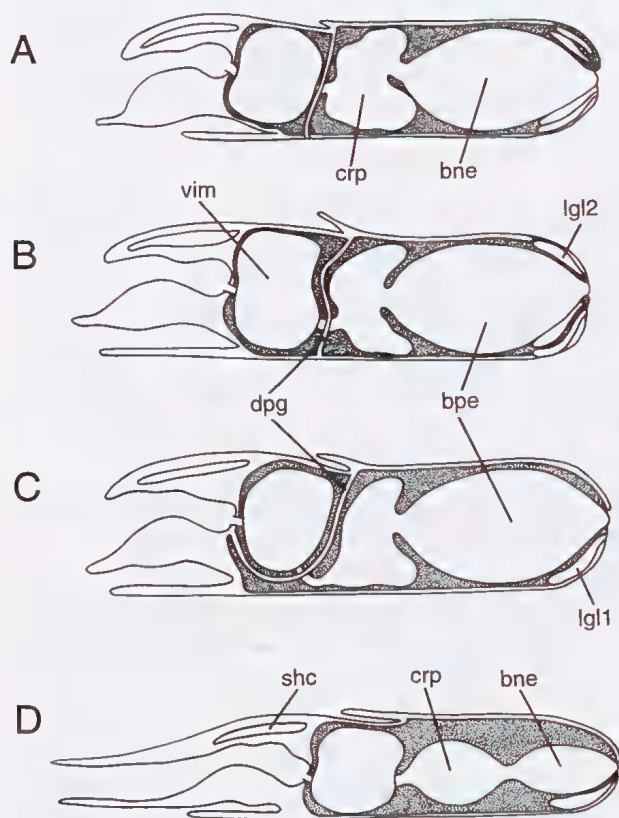


Figure 16.8 Diagrammatic view of the body cavity (haemocoel) in genera of the cephalaspidean family Aglajidae, illustrating the evolution from the primitive condition in which the anterior foregut and posterior visceral haemocoels are separated by a fibrous diaphragm (*Melanochlamys*), to the single haemocoel typical of the nudibranchs. **A**, *Melanochlamys*. **B**, *Philinopsis*. **C**, *Aglaja*. **D**, *Chelidonura*. bne, buccal bulb not eversible; bpe, buccal bulb partially eversible; crp, crop; dpg, diaphragm; lgl1, labial gland type 1; lgl2, labial gland type 2; shc, shell cavity; vim, organs of visceral spiral. (After Rudman 1974) [D. Wahl]

At about the same time, Stimpson (1853–1854), collected many marine invertebrates in Sydney Harbour during the visit of the United States naval vessel *Vincennes*. From these collections, Stimpson (1855) described four species of nudibranch and gave descriptions (although very brief) of living animals. Unfortunately the specimens have been destroyed, so their identity is also problematic.

The most valuable work at this time was that of the explorer and illustrator, George French Angas, who was employed at the Australian Museum during the 1850s. From 1858 to 1860 he collected, examined, painted accurate colour illustrations and prepared descriptions of 30 nudibranchs from the Sydney region, many of which were new species (see Fig. 1.9). This work, published in the French malacological *Journal de Conchyliologie* (Angas 1864), still represents the most accurate account of the nudibranch fauna of Sydney. Although modern taxonomy has resulted in many generic changes for Angas' species, almost all are clearly recognisable. Even if the specimens were preserved, they no longer exist, but Angas' water colour paintings are held in the Australian Museum, Sydney.

Between 1880 and 1905 about twelve new species were described from Australia, and the anatomy of a few others reported. These studies were all published by foreign workers, chiefly the Danish anatomist Rudolph Bergh, whose reputation was such that visiting and resident naturalists automatically sent nudibranch material to him. Although a diligent anatomist, his work and descriptions were basically only as good as the descriptions of the live animals sent to him by the collectors. For this reason the identity of many of these species is also problematic.

The second substantial study by resident workers was that of Basedow and Hedley on the nudibranchs of South Australia, published in 1905. They summarised the 16 species known from Australia at that time, and described and illustrated six new species in some detail. For the next 25 years the only work on the Australian fauna was by foreign workers.

Since 1931, when Joyce Allan of the Australian Museum published her first account of east coast nudibranchs, there has been at least one resident opisthobranch worker in Australia. Allan described some 18 species before retiring in 1957, the year Robert Burn of Victoria published the first of his many papers on the nudibranch fauna of Australia, especially of the south-east. Today William B. Rudman is based at the Australian Museum, Sydney, and Richard C. Willan is at the Northern Territory Museum, Darwin. As well as these full-time professionals, the beauty of opisthobranchs has attracted the interest of SCUBA divers and other students of marine life. Publications such as those of Willan & Coleman (1984) and Coleman (1989) are indicative of the growing popular interest in these animals.

Checklists of the dorid nudibranchs (Burn 1975) and more recently of all the Australian nudibranchs (Willan & Coleman 1984) have been published. The latter work lists about 300 species. Many more species are yet to be described and it is probable that within a decade the number of species known from Australia will approach 1000. In other opisthobranch groups such as the shelled cephalaspids, little work has been done in Australia or elsewhere in the tropical Indo-West Pacific. Nudibranch numbers for the Australian fauna are variously estimated to be from 2000–3000 or 4000–5000 species.

Very little is known about the basic biology of Australian opisthobranchs but the present interest in the group and the presence of resident workers has encouraged postgraduate students in some Australian universities to undertake studies on various aspects of opisthobranch biology.

The history of research into Australian opisthobranchs cannot, however, be studied in isolation, particularly because a large proportion of the opisthobranch fauna of Australia is of tropical Indo-West Pacific origin. In the simplest case, a species found for the first time in Australia has to be compared with all related species previously described from Australia and with all species

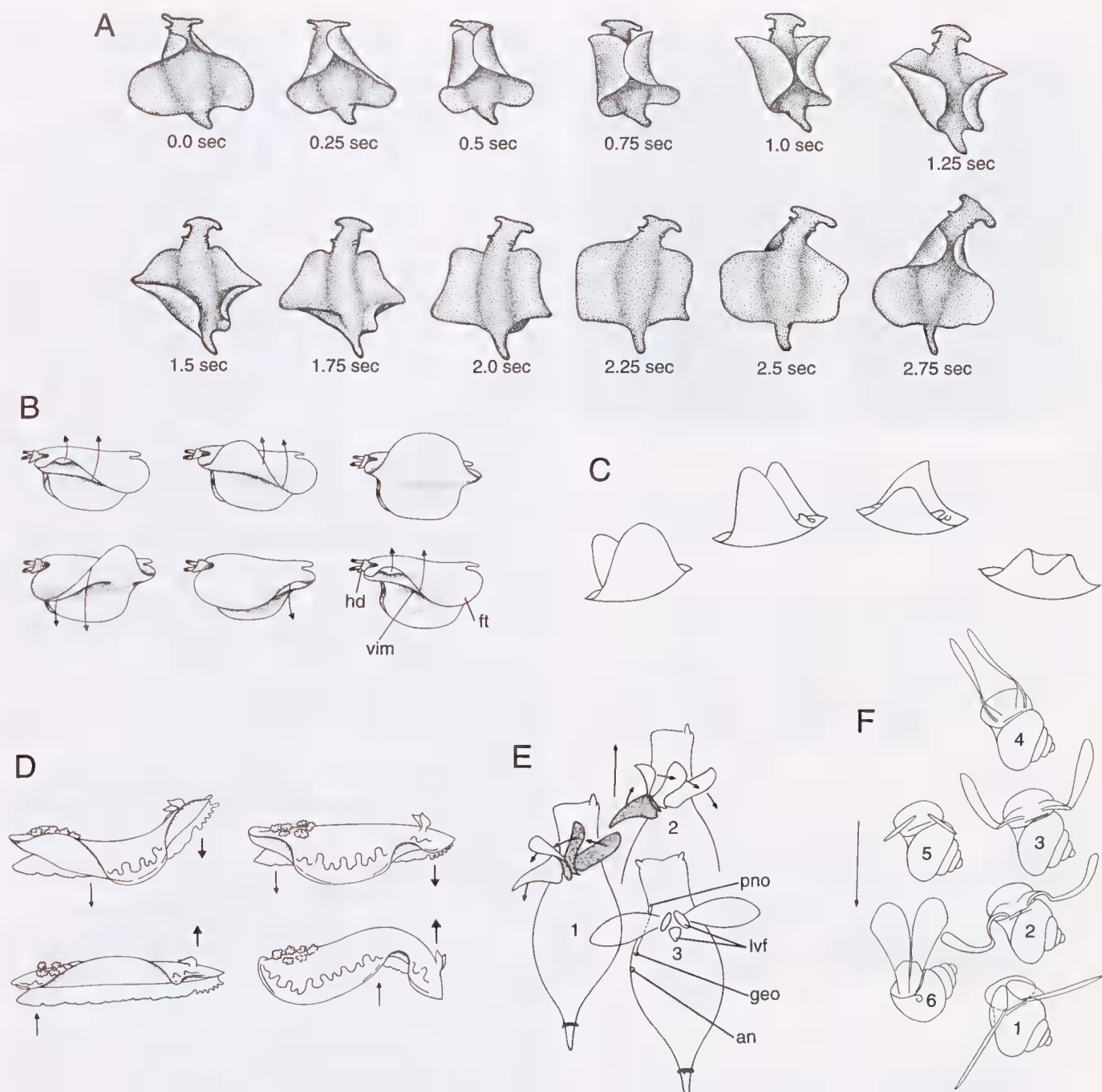


Figure 16.9 Swimming behaviour of some opisthobranchs. **A**, the European *Aplysia fasciata* (Aplysiidae), swimming movements at 0.25 second intervals show a combination of parapodial 'flapping' and a contractile wave along each parapodium. **B**, the European *Pleurobranchus membranaceus* (Pleurobranchidae), viewed from the right side (gill removed), swims with the body upside down and the mantle lobes folded down unused, while muscular waves run along the lateral extensions of the foot. **C**, the philinoidean, *Sagaminopteron ornatum* (Gastropteridae), swims using its large parapodial wings. **D**, the dorid nudibranch, *Hexabranchius sanguineus* (Hexabranchidae), commonly known as the Spanish dancer swims for extended periods by a combination of rhythmic mantle waves and dorso-ventral flexions of the body. **E**, the gymnosome pteropod, *Clione limacina* (Clionidae), swims by waving its wings backwards and forwards; this is termed 'sculling'. **F**, the thecosome pteropod, *Limacina retroversa* (Limacinidae), swims by using its large parapodial wings. an, anus; ft, foot; geo, genital opening; hd, head; lvf, lobes of vestigial foot; pno, penial opening; vim, visceral mass. (A, after Thompson & Slinn 1959; B, after Beddington & Hughes 1973; C, after Tokioka & Baba 1964; D, after Edmunds 1968b; E, after Morton 1958a; F, after Morton 1954) [D. Wahl]

previously described from the tropical Indian and western Pacific Oceans before it can be considered new to science. In special groups, in which species are known to live and feed exclusively on ascidians, bryozoans and other colonial organisms which commonly foul the bottom of boats, it is necessary to study all described species worldwide, for their present geographical distribution may be the result of human intervention.

The history of opisthobranch research in the Indo-West Pacific follows a similar but more complex pattern than that outlined above for Australia. First, specimens were collected on early European expeditions and transported to Europe for description by anatomists with no knowledge of the shape and colour of the living animals and no concept of the diversity of the faunas they were dealing with. Communication between scientists in Europe

was poor and often the same species was described independently a number of times. At the time, large collections were being sent to Europe for description, or being described in isolation in far-flung outposts of various European empires.

With the growth of colonies such as Australia, resident naturalists began to describe local faunas but many of their descriptions lacked the detail now known to be necessary for accurate species definition. Although some material, even from the early 19th century still survives in European museums, specimens without shells are so distorted and decolourised that they are of little use today. Eventually, resident workers became established with the facilities to collect and study living animals and compare them with specimens collected elsewhere in the world.

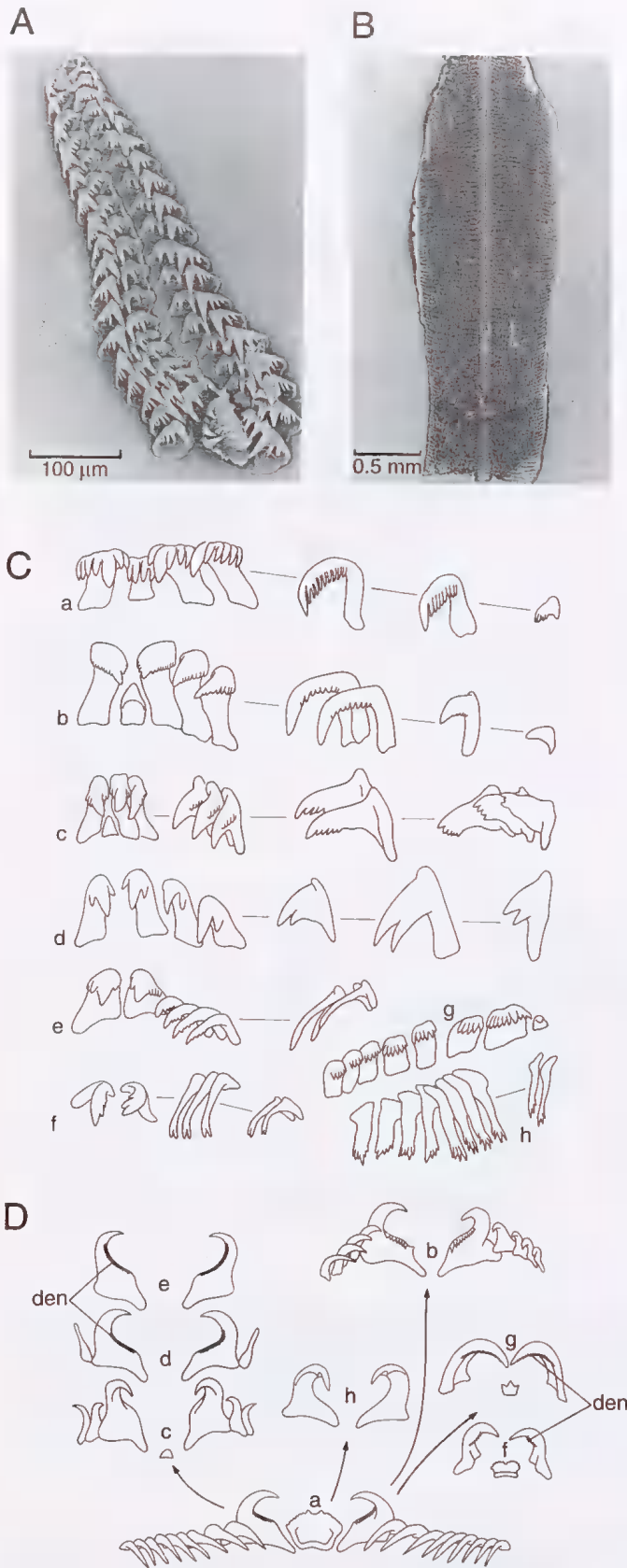


Figure 16.10 Variation in opisthobranch radular morphology. **A**, the radular of *Trapania aureopunctata* (Goniodorididae); note there is no rhachidian tooth, only two lateral teeth in each row (formula 1-0-1). **B**, the radular of *Glossodoris rufomarginata* (Chromodorididae); note numerous teeth in each radular row. **C**, variation of radular tooth shape in chromodoridid nudibranch genera (not drawn to scale): **a-f**, the innermost lateral tooth on each side and some typical teeth on the right side of a half row are shown; **g**, a complete half row on the left side and the median tooth are shown – **a**, *Cadlina*; **b**, *Glossodoris*; **c**, *Chromodoris*; **d**, *Hypselodoris*; **e**, *Noumea*; **f**, *Thorunna*; **g**, *Pectenodoris*; **h**, *Ardeadoris*. **D**, trends to simplification of the radula in the cephalaspidean superfamily Philinoidea: **a**, *Cylichna thetidis*; **b**, *Gastropteron bicornutum*; **c**, *Philine gibba*; **d**, *Philine auriformis*; **e**, *Philine angasi*; **f**, *Tornatina candei*; **g**, *Scaphander lignarius*; **h**, *Odontoglossa guamensis*. **den**, denticles. (**C**, after Rudman 1984a; **D**, after Rudman 1978) [A, B, G. Averm; C, R. Plant; D, D. Wahl]

MORPHOLOGY AND PHYSIOLOGY

External Features and Shells

Among opisthobranchs, nudibranchs are morphologically the most distinctive, as loss of the shell and subsequent elaboration of body shape and development of spectacular colour patterns set them apart from most other gastropods. All orders, however, show some stages in the evolutionary development from a shelled snail to an unshelled slug (Figs 16.1, 16.2, 16.3).

Members of the Cephalaspidea usually have an anterior head shield, devoid of tentacles and divided posteriorly into a pair of rounded lobes. The foot is relatively short and often extends laterally into a pair of parapodia which fold up in more primitive genera partially enclosing the large, external calcareous shell. Gradual loss of the shell is seen in many lineages. In the Acteonidae, the shell is spirally coiled, heavily calcified and the animal is able to retract into it completely when disturbed (Fig. 16.4A). Often a chitinous operculum is also present. In the related Bullinidae and Hydatinidae (Fig. 16.3A–C), the shell has become thinner and although the colourful animal can still retract into it, the parapodial lobes are large and partially enclose the shell, and the posterior lobes of the anterior head shield are very elaborate (Fig. 16.4B). The primitive cephalaspidean, *Cylindrobulla*, has a large external shell like *Cylichna*. In the Philinidae and Aglajidae, the body is often brightly coloured, and the shell is reduced and usually internal (Fig. 16.4C, D). Within the Gastropteridae, the shell, when present, is reduced to a thin flexible internal structure, and the parapodia are developed into large wing-like lobes which are sometimes used for swimming (Fig. 16.4D).

Similarly, stages in the evolution of a ‘slug’ are seen in the Sacoglossa. However, in advanced forms, the sacoglossan shell has become progressively smaller and the body more elaborate. Unlike that of the Cephalaspidea, though, the sacoglossan shell never becomes an internal structure. The strangest shell design is seen in the bivalved genera, *Berthelinia* and *Julia*, in which the single gastropod shell has evolved into a pair of valves into which the animal can retract completely.

The more advanced sacoglossans retain no trace of the shell in the adults and the body develops structures which in many ways are reminiscent of structures seen in the Nudibranchia. In *Elysia* and *Plakobranchus*, the sides of the foot have enlarged into parapodia which fold up and over the dorsal surface of the animal, while in *Stiliger* and *Cyerce*, tubular, spherical or flattened ceratal-like extensions of the body are arranged in dorsal and dorso-lateral clusters down the body. The head is distinguished by the development of a pair of head tentacles, usually enrolled, which are often called ‘rhinophores’ although homology with the rhinophores of nudibranchs or with the two pairs of cephalic tentacles in anaspideans is not established.

The Anaspidea (Fig. 16.3D) are distinguished by the two pairs of enrolled cephalic tentacles and the large parapodial lobes that enclose the mantle cavity. The shell is a reduced, flattened plate, either completely or partially enveloped in the mantle fold.

The Notaspidea (Fig. 16.3E) (as the common name ‘side-gilled slugs’ suggests) are characterised by the presence of a large gill along the right side of the body. In the primitive genus *Tylodina*, and the genus *Umbraculum*, a large limpet-like external shell protects the dorsal part of the slug and covers the mantle cavity. In most other notaspideans the shell is a reduced, internal plate and the consequent loss of the mantle cavity has left the gill on the right side of the body in the space between the dorsum and the foot. In notaspideans the anterior corners of the head are triangular and bear a ventral groove which is perhaps a homologue of the anterior pair of cephalic tentacles found in anaspideans. There is also a pair of enrolled dorsal cephalic tentacles.

The ‘pteropods’ (a long-established, but no longer accepted grouping of two unrelated orders) are uniquely adapted for their pelagic life style, with modified parts of the foot forming a pair of

wings used in flotation and locomotion (see Fig. 16.9E, F; Pl. 34.5). The order Thecosomata contains forms which either retain an external shell or have a thin internal gelatinous 'shell'. Thecosomes are usually small and their 'shell' is thin and fragile. The most common of the shelled pteropods are members of the Euthecosomata, which have either large spirally coiled shells (*Limacina*), or bilaterally symmetrical shells of various shapes (*Clio*, *Cavolinia*, *Diacria*). The more primitive members of the second group, the Pseudothecosomata, also have a spirally coiled external shell (*Peraclis*), but the more advanced species (*Cymbulia*, *Gleba*) have an internal pseudoconch (Lalli & Gilmer 1989). The enlarged foot of euthecosomes forms a pair of lateral wings and two pairs of smaller lobes. In some genera (*Cavolinia*, *Diacria*), large wing-like mantle lobes also occur but are seldom reported in anatomical accounts because they are extended only in the live animal. The main anatomical features distinguishing pseudothecosomes are the wings fused into a single plate, a pair of symmetrical head tentacles and the proboscis formed from part of the modified lobes of the foot.

Species in the second 'pteropod' group, the Gymnosomata, resemble snails even less than do the Thecosomata. The shell is completely absent in the adult, the head is reduced, and the 'neck' region bears three small foot lobes and a larger pair of ventral wings. One or two ciliated bands often occur around the circumference of the large conical or spherical sac-like body, and the mantle cavity is lost. These voracious carnivores catch and feed on thecosomes, using a large eversible proboscis, or, in the Pneumodermatidae, large suckered feeding tentacles more reminiscent of those of cephalopods than gastropods.

The true nudibranchs, like gymnosomes, lack a shell as adults. Most are bilaterally symmetrical, benthic, crawling slugs and most have a pair of dorsal sensory cephalic tentacles (rhinophores, see

Fig. 16.17A, E–Q). The mantle cavity has been lost; and the dorsal surface of the body, often called the 'mantle' or the 'dorsum', is considered to be homologous with the mantle of shelled species. The great diversity of external body forms is best indicated by briefly describing the features of the four main suborders.

The Doridina, commonly known as 'dorids' (Fig. 16.3F), often have the dorsum extending out around the edge of the body as a flap or brim. The rhinophores are either smooth or lamellate and the gills usually form a circle around the anus in the postero-dorsal mid-line. The head has a pair of triangular or conical oral tentacles.

The Dendronotina (Fig. 16.3G) are usually elongate and the edge of the dorsum is developed into a set of unbranched tubular 'cerata' and/or dendritic 'gills'. The rhinophores are characteristically sheathed and usually have a set of upright branches while the head usually has a bilobed oral veil. The anus opens on the right side of the body and no separate gills are present.

The Arminina (Fig. 16.3H) are flattened, elongate slugs in which the rhinophores usually bear vertical or oblique lamellae. The dorsum usually overhangs the body down each side, and beneath this skirt there are folds of the body wall which have evolved into gills.

The fourth group, the Aeolidina (Fig. 16.3I, J), is characterised by a pair of tactile oral tentacles and a pair of chemosensory rhinophores. There are no gills and in most there is no remnant of the 'mantle' skirt. Most characteristic of aeolids are the cerata, tubular outgrowths of the body wall, which are arranged in clusters down both sides of the body. The cerata act as gills and each contains a branch of the digestive gland.

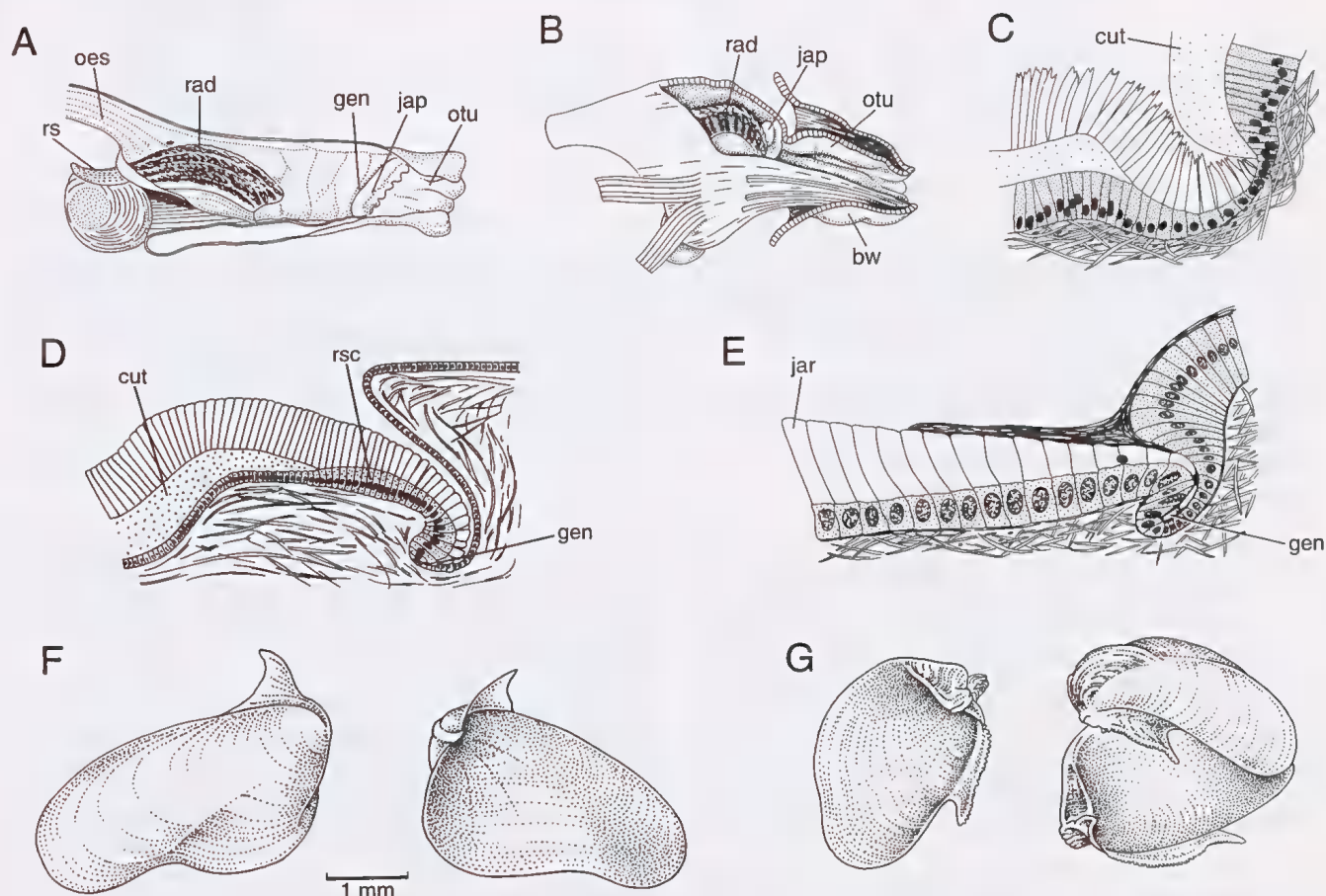


Figure 16.11 Opisthobranch jaw plates, position and morphology. **A**, sagittal section through foregut of the cephalaspid *Pupa kirki* (Acteonidae) showing the jaw plate at the anterior end of the buccal bulb. **B**, foregut of the dorid nudibranch *Rostanga arbutus* (Dorididae), with the dorsal right quarter cut away to show the jaw plate. **C–E**, transverse sections through jaw plates showing the individually secreted rodlets which are positioned in a groove along the posterior edge of each plate: **C**, *Pupa kirki* (Acteonidae); **D**, *Bulla quoyii* (Bullidae); **E**, *Haminoea zelandiae* (Haminoecidae). **F, G**, large, chitinated jaw plates of the aeolid nudibranchs: **F**, *Phestilla lugubris* (Tergipedidae); **G**, *Aeolidiopsis harrietae* (Aeolidiidae). bw, outer body wall; cut, cuticle; gen, generative groove; jap, jaw plate; jar, jaw rod; oes, oesophagus; otu, oral tube; rad, radula; rs, radular sac; rsc, red secreting cells. (**A**, after Rudman 1972h; **B**, after Rudman & Avern 1989; **C–E**, after Rudman 1971b; **F**, after Rudman 1981b; **G**, after Rudman 1982a)

[R. Plant]

16. OPISTHOBRANCHIA

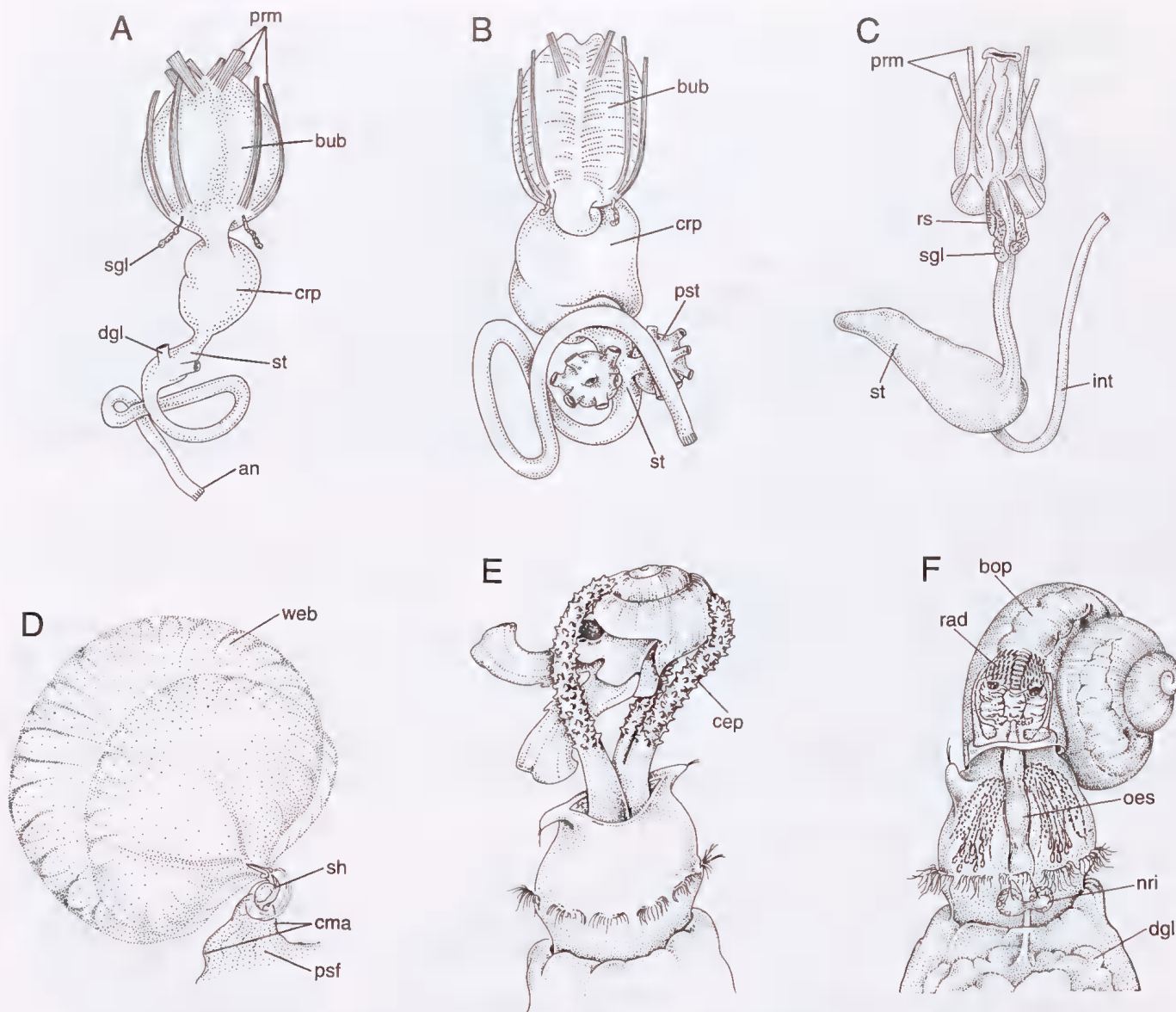


Figure 16.12 Gut morphology and feeding in the Opisthobranchia. A, B, aglajid cephalaspideans in which the radula has been lost and the buccal bulb has become a large, muscular pump for suctorial feeding; note the greatly reduced stomach, typical of most cephalaspideans: A, *Melanochlamys*; B, *Philinopsis*. C, gut of the primitive acteonid cephalaspidean, *Pupa kirkii*, which retains the 'prosobranch' sac-like stomach lost in most opisthobranchs. D, the thecosome pteropod, *Cavolinia uncinata* (Cavoliniidae), captures prey with its huge mucous web; the shell is enclosed by mantle lobes, and faeces and pseudofaeces accumulate between the mantle appendages. E, F, the gymnosomatous pteropod, *Paedoclione doliiformis* (Clionidae), capturing and eating the thecosomatous pteropod *Limacina retroversa* (Limacinidae): E, prey is captured by the everted tentacular buccal cones; F, the prey is macerated by the action of the radular after the proboscis has been everted into the shell aperture and the buccal cones have been retracted. an, anus; bop, body of prey; bub, buccal bulb; cep, cephaloconia; cma, central mantle appendages; crp, crop; dgl, digestive gland; int, intestine; nri, nerve ring; oes, oesophagus; prm, protractor muscles; psf, accumulated pseudofaeces and faeces; pst, pseudostomach; rad, radula; rs, radular sac; sgl, salivary gland; sh, shell; st, stomach; web, mucous web. (A, B, after Rudman 1972d; C, after Rudman 1972b; D, after Gilmer & Harbison 1986; E, F, after Lalli 1972)

[R. Plant]

The shell, when present in opisthobranchs, either externally or internally, is accompanied by an underlying layer of mantle. In those taxa with a visible external shell (*Pupa*, *Hydatina*), the mantle cavity opens more to the right side of the head than in most of the streptoneurous gastropods. Some of the structures (for example, the rectum and gonoduct) borne on the mantle roof of caenogastropods are found on the mantle floor of these opisthobranchs (Rudman 1972a, 1972b). Often the posterior (right) edge of the mantle becomes an enlarged and detached 'infrapallial lobe' which encloses all or part of the shell and can become a secondary posterior 'foot' (Fig. 16.5; Rudman 1971a).

The opisthobranch mantle cavity is also characterised by the presence of a pair of ciliated ridges or 'raphes', one on the floor and the other on the roof on the right side, the cilia on which create a water current through the cavity (Fig. 16.6A, B). Among lower opisthobranchs there are examples of all stages in the degeneration and loss of the mantle cavity and associated structures. As opisthobranchs tend towards a bilateral symmetry, the anus, genital openings and renal openings no longer face

anteriorly, but are found at various positions down the right side of the body. The dorid arrangement, with the anus in either the postero-dorsal mid-line or, rarely, at the posterior tip of the body (*Fryeria*), is the ultimate stage in the return to bilateral symmetry of the opisthobranch body.

The epithelial cells of most nudibranchs are characterised by the presence of many special vacuoles of unknown function (see Fig. 16.20B–D). The vacuoles are ellipsoidal and contain a flexible sac and a cylindrical axis. They have been likened to rice grains. These vacuolated cells are known at present only from nudibranchs (Schmekel 1985). The loss of the shell in opisthobranchs has been accompanied by the development of many types of epidermal glands, most of which are considered to be defensive (Thompson 1960a, 1960b; Edmunds 1966, 1968a; Rudman 1981a, 1984a). In the more primitive groups (Cephalaspidea, Anaspidea, Notaspidea), these glands (known as repugnatorial glands, Fig. 16.7A, B) produce a white, viscous, acidic secretion which is a product of the slug's own metabolism. There is now substantial evidence that the repugnatorial glands of

nudibranchs exude chemicals that have been obtained from the nudibranch's food. Among the chromodorid nudibranchs, anti-predatory chemicals, termed anti-feedants, produced by sponges for their own defence are ingested with the sponge tissue during feeding. The chemicals are stored, substantially unaltered, in the chromodorid's epithelial glands (see Fig. 16.20A for patterns), to be exuded when the slug is attacked (Rudman 1991a).

One well-known aeolid defence mechanism involves the use of undischarged nematocysts, ingested from cnidarians during feeding, and stored in specialised sacs (cnidosacs) at the tip of each aeolid cerata. When the aeolid is disturbed it is able to expel and discharge these stolen nematocysts to deter predators (see Fig. 16.20B). Thompson & Bennett (1969) provided a good account of the preferential storage by *Glaucus* of the most powerful nematocysts from the pelagic siphonophore, the blue-bottle or Portuguese man-o-war, *Physalia*.

Body Cavities

Consistent with other molluscs, the opisthobranch body cavity is not coelomic; the coelom is confined to the kidney, the pericardial sac and the ovotestis. In nudibranchs, the internal organs are found within a large continuous blood-filled cavity, best described as a haemocoel. Among the more primitive opisthobranchs (Cephalaspidea, Anaspidea), the haemocoel is usually confined to the cephalic region and the pre-stomachal region of the gut. In the Aglajidae (Fig. 16.8), genera are found showing arrangements representing various stages in the evolution of a continuous haemocoelic body cavity (Rudman 1974).

Blood in the main body cavity, and in other smaller cavities within the musculature, has, in addition to the normal functions of transport of gases, nutrients and waste products, a secondary function in providing these animals with a hydrostatic skeleton. By differential contraction and relaxation of sets of muscles the blood can be used hydraulically to evert the proboscis, elongate the body, expand the mantle edge or parapodia, and assist in the many slight changes in body shape that take place continually.

Locomotion

The opisthobranch foot resembles those of caenogastropods with mucous secretions and some ciliation; locomotion is effected by a combination of muscular waves and ciliary creeping. Among the Cephalaspidea, some families, such as the Aglajidae, rely predominantly on ciliary creeping. Species crawling on or burrowing through the upper layers of soft sediments do so with the aid of mucus from their large anterior mucous glands. A tunnel of mucus is produced through which they glide by using the constantly beating epithelial cilia found on the head shield, ventral foot and large lateral parapodial extensions of the foot (Rudman 1972c, 1972d). In many sacoglossans and hydroid-feeding aeolids which live on branching plants or dendritic animal colonies, the foot produces a viscous pedal mucus which assists the opisthobranchs to adhere during excessive water movement caused by waves or tidal currents.

Many of the shelled cephalaspideans are epifaunal burrowers and the characteristic head shield is adaptive for this mode of life. In many of the more advanced cephalaspideans in which the shell is reduced and internal, the body is streamlined and often the body wall is highly muscularised (Rudman 1972e, 1972f) for burrowing quite deeply in soft sediments. Opisthobranchs are not wholly benthic; those that are not can either swim actively (Fig. 16.9), usually for short periods, or are primarily floaters that have developed means to achieve neutral buoyancy. Among the swimmers, two swimming methods recur. The body either has developed large lateral extensions which 'flap' like wings (Fig. 16.9A–C), or large longitudinal blocks of muscle throw the whole body into a series of lateral or dorso-ventral flexions (Fig. 16.9D). In a very few forms, swimming occurs for extended periods and may be related to some communal, perhaps mating, behaviour.

The European *Pleurobranchus membranaceus* (Notaspidea) is reported to swarm periodically, many specimens aggregating in an area for some days. During swimming, the body is held upside down and the mantle is folded down into a ventral 'keel' while the now-dorsal foot extends laterally into a pair of undulating fins along which a muscular wave passes posteriorly (Fig. 16.9B). The wave on one side is in exact opposition to that on the other so that while one side is undergoing an effective swimming stroke the other side is undergoing a recovery stroke, causing the body to roll as it swims along (Thompson & Slinn 1959). The reason for these massed swimming aggregations is unknown. In *Pleurobranchus*, the extension of the foot for swimming is a temporary phenomenon caused by a combination of muscular and hydrostatic forces in the foot.

Permanent lateral extensions for swimming have evolved in other opisthobranchs. Swimming behaviour in one of these, the shelled anaspidean *Akera bullata*, was described by Morton & Holme (1955). The body is held vertically with the head up and the visceral mass hanging down while the large lateral extensions of the foot, the parapodia, are gently waved up and down in unison. This well-studied European species is very similar in shape to a sometimes very abundant Australian species, *Akera soluta*, which also has been observed to swim (R.C. Willan personal observation, at Lizard Island, Queensland).

Some species of *Aplysia* swim, including the European *Aplysia fasciata*, which uses synchronous waves passing down the enlarged parapodia (Fig. 16.9A). Two large aplysiids, *Aplysia extraordinaria* from eastern Australia, and *A. gigantea* from Western Australia, which both grow to over 400 mm in length, swim occasionally as a defensive reaction, using parapodial waves. None of the other common Australian species has been observed swimming. One remarkable development seen in anaspideans is jet propulsion. In *Notarchus punctatus*, the parapodial lobes are fused except for one small slit which can form temporary inhalant and exhalant siphons. A large volume of water is sucked into the parapodial cavity from which it is then expelled with great force, jetting the animal upwards. While refilling the cavity the animal 'somersaults' before the next exhalation of water jets it further along (Martin 1966).

Among cephalaspideans, gastropod species have also evolved large parapodial flaps for swimming. In these species, the parapodia on each side flap up and down in synchrony (Fig. 16.9C; Pl. 33.5). There is no anterior wave along the parapodia as in *Aplysia*. Again, why these opisthobranchs swim is not clear but they can often be made to swim when irritated or disturbed. Among nudibranchs, the most spectacular swimming display is produced by the large tropical dorid *Hexabranchus sanguineus* (Fig. 16.9D). Normally it crawls along the substratum like other dorids with its large dorsal skirt rolled over its dorsum. As the underside of the skirt is coloured with a dull mottled pattern, *Hexabranchus* is almost invisible against the substratum. However if disturbed, the skirt is unfolded rapidly to display a spectacular colour pattern of red and white bands. The skirt appears to increase in size and is held out laterally. At this stage, a muscular locomotor wave is generated anteriorly which passes down the body and mantle skirt, initiating a forward swimming motion. This locomotor wave is accompanied by vigorous dorso-ventral flexions of the whole body. A swimming episode can last for five minutes or longer (Edmunds 1968b). Clearly the initial response to disturbance – displaying the brilliant but hidden colours – can be interpreted as a warning display. Equally, the subsequent swimming is probably an escape response which would enable the animal to move a considerable distance from the source of the disturbance, even in a slow current.

Most other nudibranchs that have been reported to swim occasionally, do so by lateral flexion of the whole body. This involves narrowing of the body (to reduce its width and increase its height) and erection of all body protuberances in the same plane, thus increasing the size of the 'paddle' or 'oar' that is being pushed against the water. In *Melibe* (Dendronotina), the dorsal cerata, the oral hood and even the rhinophore sheaths are flattened and held erect (Pl. 36.5). Similar behaviour occurs in the related species

Bornella stellifer. Many polycerids (suborder Doridina), including many of the Nembrothinae, swim by lateral flexion. Among the Polycerinae, *Plocamopherus ceylonicus* and *P. imperialis* show anatomical and behavioural adaptations for this type of swimming. The large oral veil is held at an angle, the gills are held erect, and a dorso-medial crest at the back of the body becomes greatly narrowed laterally. Concurrently, the whole foot and body are flattened out in the same plane and at each lateral flexion the posterior tip of the body comes close to the head. This type of swimming relies basically on sheer force which can be applied with maximum effect by increasing the surface area available for each push. One species in which this mechanism is developed even further is *Bornella anguilla*, appropriately named for the lateral flexion is modified, producing a series of eel-like locomotor waves down the body (Johnson 1984).

Few nudibranchs are truly pelagic. One well-known example is *Phylliroe* (suborder Dendronotina) which is a thin, laterally flattened slug that swims by passing a locomotory wave along the body; the foot is completely lost in the adult. The two aeolids, *Glaucus atlanticus* and *Glaucilla marginata*, which feed exclusively on the siphonophores *Porpita* and *Physalia* are also pelagic. Both are very similar in anatomy and behaviour and float upside down at the water surface, buoyed up by a gas bubble in the gut (Thompson & Bennett 1970). They are able to move slightly by lateral flexion of the body and turn over if turned up the 'wrong way', but they are unable to use the foot for crawling if placed on a hard substratum without sufficient water for floating.

Among the pelagic opisthobranchs, gymnosomes are said to swim by means of a 'sculling action' (see Morton 1958a – *Clione limacina*; Lalli & Gilmer 1989). Essentially, the paired wings of gymnosomes wave in synchrony backwards and forwards, but at an angle to the direction of motion (Fig. 16.9E). By placing the wings at a different angle during the downstroke from that adopted during the upstroke, the wings are able to give a forward thrust on both strokes. This mode of propulsion can be compared with that of the shelled thecosomes which Morton (1954) likened to 'rowing a boat'. This occurs in the euthecosome genus *Limacina*, where a forward or upward thrust is achieved by a downstroke of the large parapodial wings (Fig. 16.9F). There is no active recovery stroke and when the wings are flaccid, sinking drags them back into the forward position so that they are ready for the next downstroke. This inefficient swimming method is only successful because euthecosomes have a nearly neutral buoyancy. Whereas euthecosomes pull their shell through the water, pseudothecosomes (*Peraclis*, *Cymbulia*) push their shell. The single, fused, plate-like pseudothecosome wing provides an upward movement by dorso-ventral flexion and a forward movement by an undulating wave along the plate. In slow motion the wingplate faces upward in the water and the shell is below, but during rapid movement the position is reversed.

Feeding and Digestion

The basic physiology of the opisthobranch gut is similar to that of all gastropods, but differs from that of most streptoneurous gastropods in the wide diversity of radular morphology (Fig. 16.10) found within the different groups and the development of chitinous oesophageal and stomachal armature. The structure of the radular ribbon ranges from a single tooth in each row, as found in most aeolid nudibranchs and sacoglossans, to the state in anaspideans and some dorids where each transverse row of the ribbon contains hundreds of teeth. One characteristic feature of many opisthobranchs is the presence of cuticularised jaw plates (Fig. 16.11). In many cephalaspideans, anaspideans and notaspideans and some nudibranchs, the jaws consist of a laterally placed plate on each side of the mouth within the buccal cavity (Fig. 16.11A, B). Usually the plate consists of individually secreted rodlets (Fig. 16.11C–E). In *Umbraculum* and many dorids the jaws are represented by a cuticularised ring. In some of the Dendronotina, in aeolids and in gnathodorids (suborder Doridina) the jaw plates are large, uniformly chitinated, concave plates (Fig. 16.11F, G) which enclose or partially enclose, the buccal bulb.

Loss of the radula has occurred independently a number of times within the Opisthobranchia. Among cephalaspideans, species of *Retusa* (which feed on infaunal foraminiferans and small molluscs) lack a radula but retain an oesophageal gizzard with three chitinous plates. In the Aglajidae, the loss of the radula has been accompanied by major modifications to the foregut. In *Melanochlamys* (Fig. 16.12A), the buccal bulb is modified into a massive pump to suck in polychaete worms, while in *Philinopsis* (Fig. 16.12B) it is developed into an eversible proboscis capable of engulfing other shelled cephalaspideans (Rudman 1972d). Another aglajid genus, *Odontoglaja*, has a radula (Fig. 16.10D) and a rudimentary gizzard (Rudman 1978), indicating a relationship of this family to the Philinidae.

The remarkable feeding behaviour of thecosomes (Gilmer 1972, 1974; Gilmer & Harbison 1986), in which plankton is caught in large mucous webs and sorted in ciliary pathways on the mantle, still involves a radula and jaw plates. The radula, consisting of a few rows of three teeth, pulls the strands of mucus and food into the gut. Lateral jaw plates consist of aggregations of cuticular rods. In euthecosomes, the mucous web is spherical while in pseudothecosomes it is usually funnel-shaped or a flattened sheet (Fig. 16.12D). Pseudothecosomes have a proboscis which is long and extensible in some genera (*Corolla*, *Gleba*). Most have a radula with three to five teeth per row (*Cymbulia*, *Peraclis*) but in *Gleba* and *Corolla* both the radula and jaws have been lost (Lalli & Gilmer 1989).

The feeding organs of gymnosomes show great diversity (Fig. 16.12E, F), perhaps associated with their actively carnivorous feeding behaviour. All except one deepwater species, *Laginopsis trilobata*, retain the radula which consists of a wide serrated central tooth flanked by up to 15 hooked teeth on each side, similar to those of philinids. As in thecosomes, jaw plates are usually present. The large paired hook-sacs found on each side of the radula are unique to gymnosomes. These large eversible sacs contain up to 100 curved, chitinous hooks which can be protruded from the mouth during feeding. More details of their structure and function are given by Lalli & Gilmer (1989).

The radula has been lost in the nudibranch genus *Melibe* (Dendronotina), which has a large oral hood used to catch small crustaceans (Pl. 36.5; Hurst 1968). It has also been lost in two dorid families, Dendrodoridae and Phyllidiidae, which both feed suctorially on sponges.

An oesophageal gizzard has evolved in many cephalaspidean groups. In the herbivorous Haminoeidae, a set of three large chitinous plates held together by a broad muscular band (Rudman 1971b, 1972g) is used to grind the ingested plant tissue (Fig. 16.13A–C). The Bullidae also have a gizzard with three chitinous plates but the anatomy (Fig. 16.13D) suggests that the plates are used for crushing rather than grinding. The gizzard of *Bulla* species also has cuticularised papillae at its entrance and exit. Another herbivorous group, the family Runcinidae (Fig. 16.13E–G), has a grinding gizzard which is unique in having four chitinous plates (Miller & Rudman 1968; Rudman 1971b). Among the carnivorous cephalaspideans many of the small shelled families have three chitinous gizzard plates which assist in crushing the prey. Species of *Retusa*, in which the radula is lost, still retain the gizzard. In the genus *Philine* (Fig. 16.14), an array of species shows a progression from small chitinous gizzard plates and a relatively large radula to species such as *Philine angasi* (Fig. 16.14A–E), in which the radula is relatively small and the large, strongly calcified gizzard plates are capable of crushing heavily calcified bivalve shells (Rudman 1972e, 1972f).

By comparison, the oesophageal gizzard in the herbivorous anaspideans has two regions (Fig. 16.13H). The anterior crushing or grinding section has a number of large chitinous pyramids surrounded by a thick muscular band. In the posterior sieving section, the gut wall is only thinly muscularised and many small narrow chitinous spines and plates block the entrance to the stomach. A similar oesophageal gizzard, with a number of chitinous plates is found in most thecosomes, but is lacking in gymnosomes.

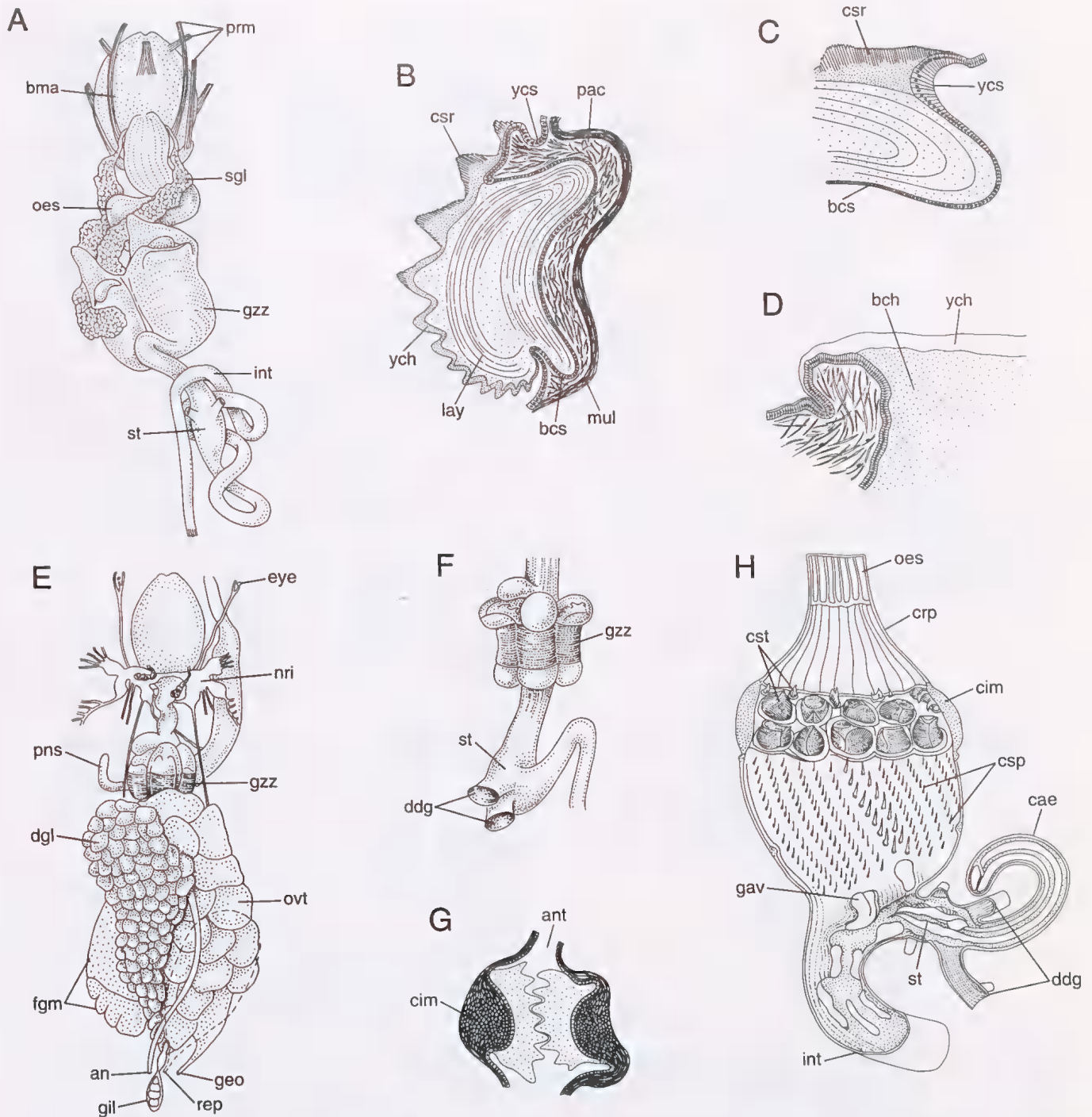


Figure 16.13 Gizzards and gizzard plates of herbivorous cephalaspidean (A–G) and anaspidean (H) opisthobranchs. A–C, *Haminoea zelandiae* (Haminoecidae): A, gut showing position of gizzard; B, longitudinal section through a gizzard plate; C, longitudinal section through the posterior end of the gizzard plate. D, *Bulla quoyii* (Bullidae), longitudinal section through the posterior end of the gizzard plate. E–G, *Runcina katipoides* (Runcinidae): E, gut showing position of gizzard; F, gizzard showing the position of three of the four gizzard plates; G, longitudinal section through the gizzard. H, *Dolabella auricularia* (Aplysiidae), oesophageal crop and stomach region opened dorsally to show the armature of the gizzard. an, anus; ant, anterior; bch, blue chitin; bcs, blue chitin secretory layer; bma, buccal mass; cae, caecum; cim, circular muscle band; crp, crop; csp, chitinous spines; csr, chitinous rods; cst, chitinous teeth; ddg, digestive gland ducts; dgl, digestive gland; eye, eye; fgm, female gland mass; gav, gastric valve; geo, genital opening; gill, gill; gzz, gizzard; int, intestine; lay, layering; mul, muscle layer; nri, nerve ring; oes, oesophagus; ovt, ovotestis; pac, packing tissue; pns, penial sac; prm, protractor muscles; rep, renal opening; sgl, salivary gland; st, stomach; ych, yellow chitin; ycs, yellow chitin secretory layer. (A–G, after Rudman 1971b; H, after Fretter & Ko 1979) [R. Plant]

In the Notaspidea, the so-called ‘stomach’ wall can bear chitinous armature (Hyman 1967; Schmekel 1985), but as the digestive gland opens after these structures they could be homologous with the oesophageal gizzard plates of cephalaspideans and anaspideans.

Among nudibranchs, only the Dendronotina bear chitinous armature. However, this usually consists of a transverse band of plates or triangular lamellae just posterior to the digestive gland openings into the stomach. This armature appears to form a

barrier preventing large particles from entering the intestine and it is probably not homologous with the oesophageal gizzard described above.

Chitinous structures developed from the lining of the alimentary canal are widespread among opisthobranchs and probably reflect a primitive ability of the epithelial cells of the alimentary canal to secrete a chitinous layer. This is illustrated in the acteonids *Pupa* and *Maxacteon* in which the oesophagus and stomach are lined with a thin cuticle (Rudman 1972h). A similar anatomy is described in the related *Hydatina* and *Bullina* by Rudman (1972i, 1972a).

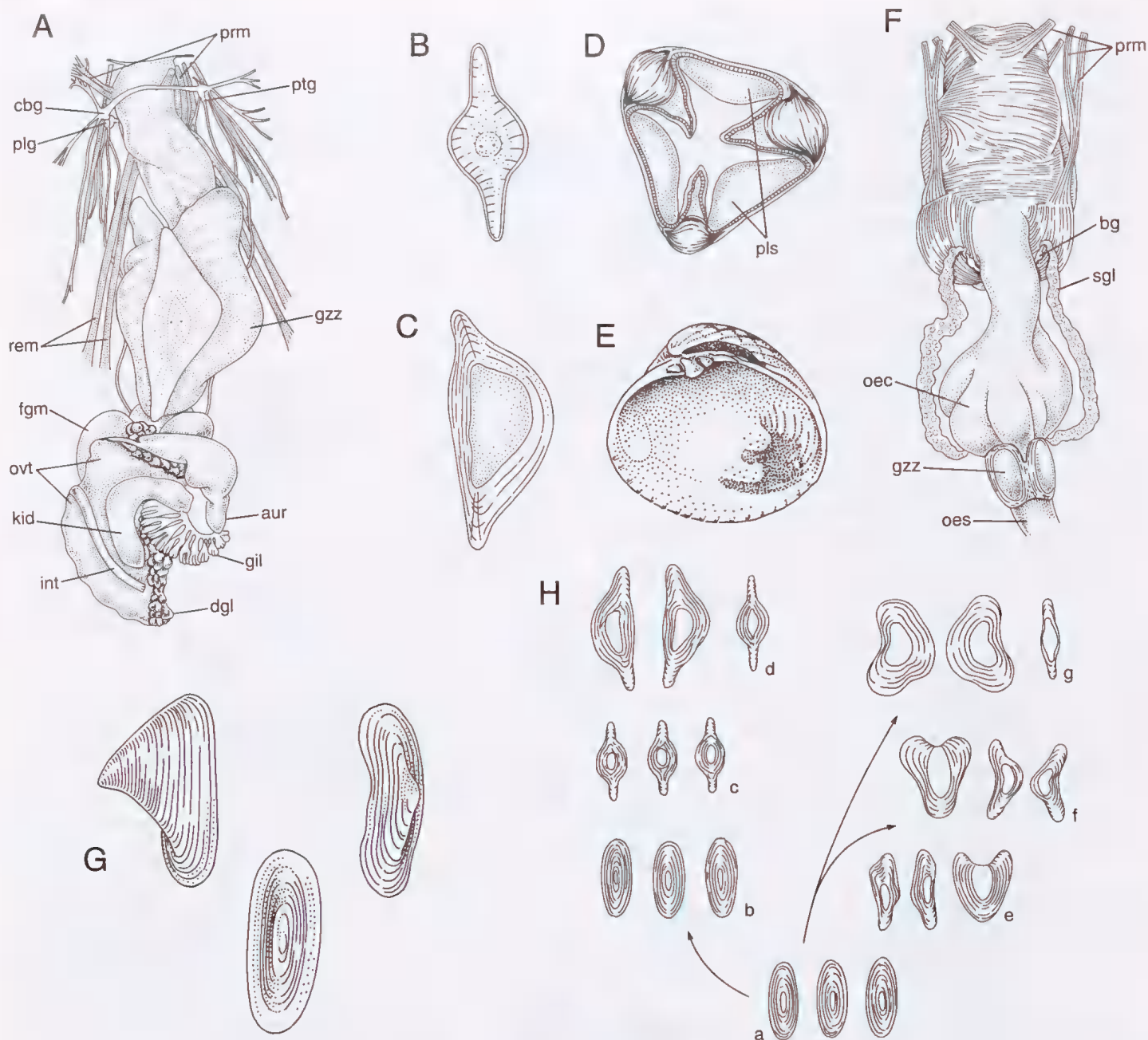


Figure 16.14 Gizzards and gizzard plates of carnivorous philinoidean cephalaspideans. **A–D**, *Philine angasi* (Philinidae): **A**, foregut showing the large oesophageal gizzard; **B**, **C**, two of the three gizzard plates showing the two different shapes present; **D**, transverse section of the gizzard showing the positions of the three calcareous gizzard plates (**B–D** all drawn to the same scale). **E**, the gizzard plates are able to crush large bivalves such as *Chione* species. **F**, **G**, *Philine falklandica* (Philinidae), illustrating a presumably more primitive state with a small gizzard (**F**) containing three chitinised (**G**), not calcified gizzard plates. **H**, trends in the evolution of gizzard morphology: **a**, *Cylichna thetidis*; **b**, *Philine gibba*; **c**, *Philine uriformis*; **d**, *Philine angasi*; **e**, *Cylichnella bidentata*; **f**, *Tornatina canaliculata*; **g**, *Scaphander lignarius*. **aur**, auricle; **bg**, buccal ganglion; **cbg**, cerebral ganglion; **dgl**, digestive gland; **fgm**, female gland mass; **gill**, gill; **gzz**, gizzard; **int**, intestine; **kid**, kidney; **oec**, oesophageal crop; **oes**, oesophagus; **ovt**, ovotestis; **plg**, pleural ganglion; **pls**, plates; **prm**, protractor muscle; **ptg**, parietal ganglion; **rem**, retractor muscles; **sgl**, salivary gland. (**A–E**, after Rudman 1972e; **F**, **G**, after Rudman 1972f; **H**, after Rudman 1978) [R. Plant]

Circulation and Respiration

Like other gastropods, opisthobranchs have an open circulatory system in which the movement of blood is at least partially dependent on a two-chambered heart (Fig. 16.15). The heart receives blood from large venous sinuses, and pumps it out through arteries to the body organs and tissues. It then passes again to the venous sinuses, which are often ill-defined cavities in the musculature and around the body organs. In the more primitive cephalaspideans there is a large cephalic sinus which partially surrounds the foregut. In the more advanced cephalaspideans (Aglajidae), in which the reduced shell is internal and the viscera are enclosed in a muscular body wall, there is a second cavity in which the viscera lie bathed in blood. The two cavities are separated by a thin vertical fibrous wall or diaphragm (Fig. 16.8A–D; Rudman 1974). More advanced opisthobranchs, such as nudibranchs, have all the body organs contained in one

blood-filled body cavity. This is not a true coelomic cavity and is more appropriately termed a haemocoel. The haemocoel, as well as having a circulatory role, also functions in providing a hydrostatic skeleton (see section on Body Cavities above). Anatomical changes to the vascular system during the transition from caenogastropod to heterobranch organisation are discussed in detail by Brace (1977b).

At the base of the gill or gills, a sinus connects the gills with the haemocoelic blood. A second sinus enables haemocoelic blood to enter the kidney directly. The ducts carrying blood from both the gills and the kidney join to form a single duct emptying into the auricle (Fig. 16.15B), the first chamber of the heart. The cycle is complete when the muscular ventricle pumps the blood back into the body through the main aorta. This is clearly an open system: the blood, having passed through the kidney, is passed back into the body without passing through the gills. There is also no

systematic way in which the blood in the haemocoel is passed through the gills in any regular sequence. Clearly the bigger the haemocoelic cavity the more inefficient the circulatory system. Perhaps this is why many nudibranchs have thin body walls which probably allow considerable gas exchange through the body wall directly into the haemocoel. Among aeolids and the nudibranch-like limapontiid sacoglossans, examples can be found of rhythmic ceratal pumping; the cerata function as secondary hearts. In one sacoglossan, the European *Alderia modesta*, the heart and pericardium are completely lost and blood circulation is entirely dependent on ceratal pumping.

In this brief review of circulation and respiration, one enigmatic organ, 'the blood gland' (Fig. 16.15C), does deserve a mention. It has been described commonly from cephalaspideans, notaspideans and from dorid nudibranchs and is often a conspicuous follicular gland mass attached to the anterior aorta. The function of the gland is unknown but it has been suggested that it is associated with the production of amoebocytes (Schmekel & Weischer 1973).

A question of considerable phylogenetic importance is whether all opisthobranch gills are homologous, and if so, is the opisthobranch gill homologous with the true molluscan ctenidium. There is considerable variation in gill structure among opisthobranchs. In many shelled sacoglossans, the gill consists of a few folds of the mantle roof, but in most shelled cephalaspideans it is a discrete organ, usually elongate triangular in shape, attached basally to the mantle roof and consisting of a folded layer of the mantle. A gill of similar shape is found in anaspideans but it is more complex within the Notoaspidea. In aeolidiform nudibranchs, the gill is completely lost, and in dorids it has become a circlet around the anus.

The position of the gill relative to the other mantle organs is comparable to that of streptoneuran gastropods, and consequently Hoffmann (1940) considered that the opisthobranch gill is homologous with the streptoneuran ctenidium. Morton (1972) reviewed the morphology of opisthobranch gills and concluded that their lack of skeletal support and absence of characteristic ciliation show that they represent a 'new' opisthobranch organ which he named the 'plicatidium'. However many workers, on anatomical grounds (see Schmekel 1985 for review), embryological grounds (Tardy 1970), and fine structure (Jonas 1984, 1986), support the earlier view that the opisthobranch gill, while often very specialised, is a true ctenidium. More recent studies on aspects of gastropod phylogeny (Haszprunar 1988) support the view that the heterobranch gill is a new structure. Neither opinion is supported by convincing evidence.

Sense Organs and Nervous System

The opisthobranch and pulmonate gastropods have long been considered separate from other gastropods because of the nature of the nervous system. One of the earliest classifications divided the Gastropoda into the Streptoneura ('prosobranchs') and the Euthyneura (opisthobranchs and pulmonates) on the basis of the form of the nerve ring. In the Streptoneura, the visceral nerve ring is twisted into a figure eight as a result of the twisting of the initially bilaterally symmetrical animal during torsion. The nerve ring in the Euthyneura is in a 'detorted' bilaterally symmetrical state. Among opisthobranchs, all but a few primitive shelled groups have a euthyneurous nervous system (Fig. 16.16C–G, I, J). Those groups that still retain a 'torted' streptoneurous system (Fig. 16.16A, B, H) include Acteonidae, Hydatinidae, Bullinidae (Rudman 1972a, 1972b, 1972i); and *Akera* (Anaspidea) (Kandel 1979).

The opisthobranch nervous system is characterised by a ring of large ganglia around the anterior end of the gut (Figs 16.13E, 16.14A, 16.16K). There is a pair of dorsally placed cerebral ganglia joined to each other by a cerebral connective or commissure. Below each cerebral ganglion is a pedal ganglion joined by a cerebro-pedal commissure to the cerebral ganglion above, and by a

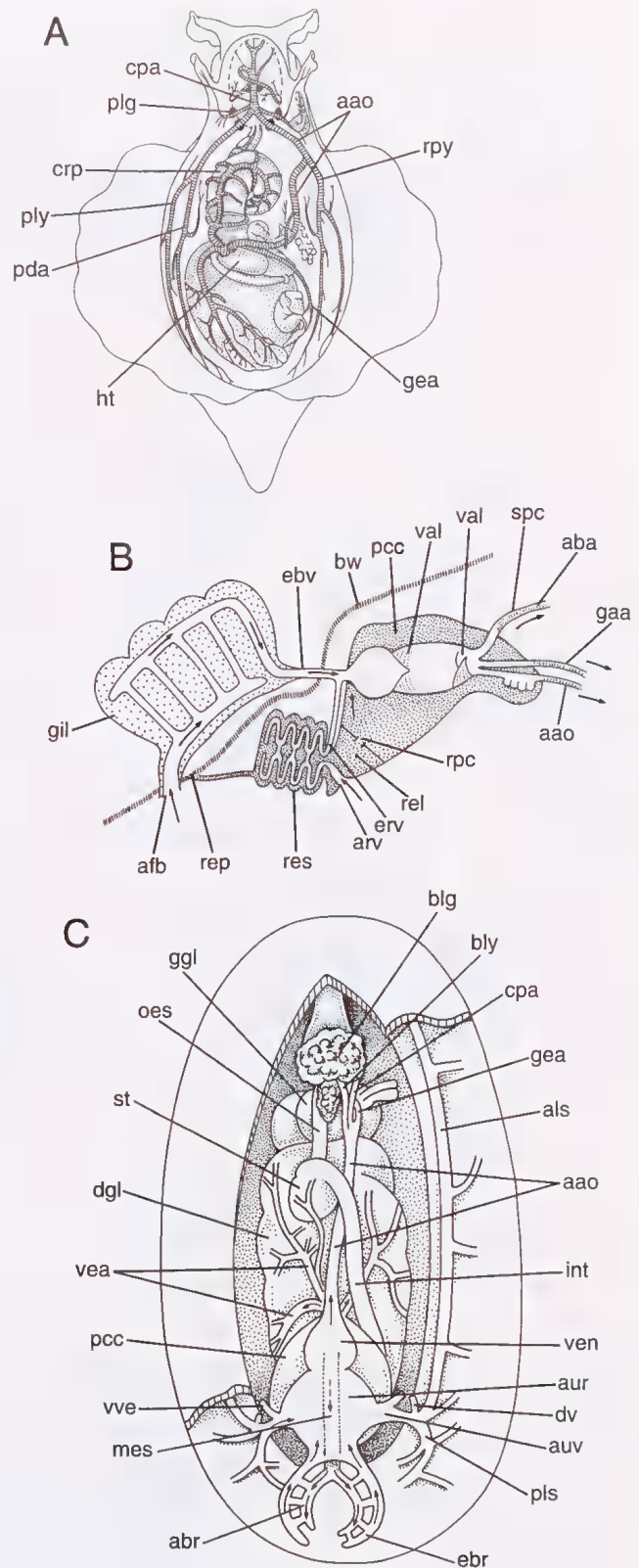


Figure 16.15 Circulatory systems of some opisthobranchs. A, *Aplysia californica* (Aplysiidae). B, *Aplysia* sp., blood flow through gill, kidney and heart. C, *Platydorid* sp. (Dorididae). aao, anterior aorta; aba, abdominal aorta; abr, afferent branchial ring; afb, afferent branchial vein; als, anterior lateral sinus; arv, afferent renal vein; aur, auricle; auv, auricular vein; blg, blood gland; bly, blood gland artery; bw, body wall; cpa, cephalic artery; crp, crop; dgl, digestive gland; dv, dorsal vein; ebr, efferent branchial ring; ebv, efferent branchial vein; erv, efferent renal vein; gaa, gastro-oesophageal artery; gea, genital artery; ggl, genital gland mass; gil, gill; ht, heart; int, intestine; mes, medial sinus; oes, oesophagus; pcc, pericardial cavity; pda, pedal artery; plg, pleural ganglion; pls, posterior lateral sinus; ply, parapodial artery; rel, renal coelom; rep, renal pore; res, renal sac; rpc, renopericardial duct; rpy, right pedal and parapodial artery; spc, sphincter; st, stomach; val, valve; vea, visceral arteries; ven, ventricle; vve, ventral vein. (A, after Robinson in Kandel 1979; B, after Mayeri, Koester, Kupfermann, Liebeswar & Kandel 1974; C, after composite drawing, modified from García & García-Goméz 1990) [R. Plant]

16. OPISTHOBRANCHIA

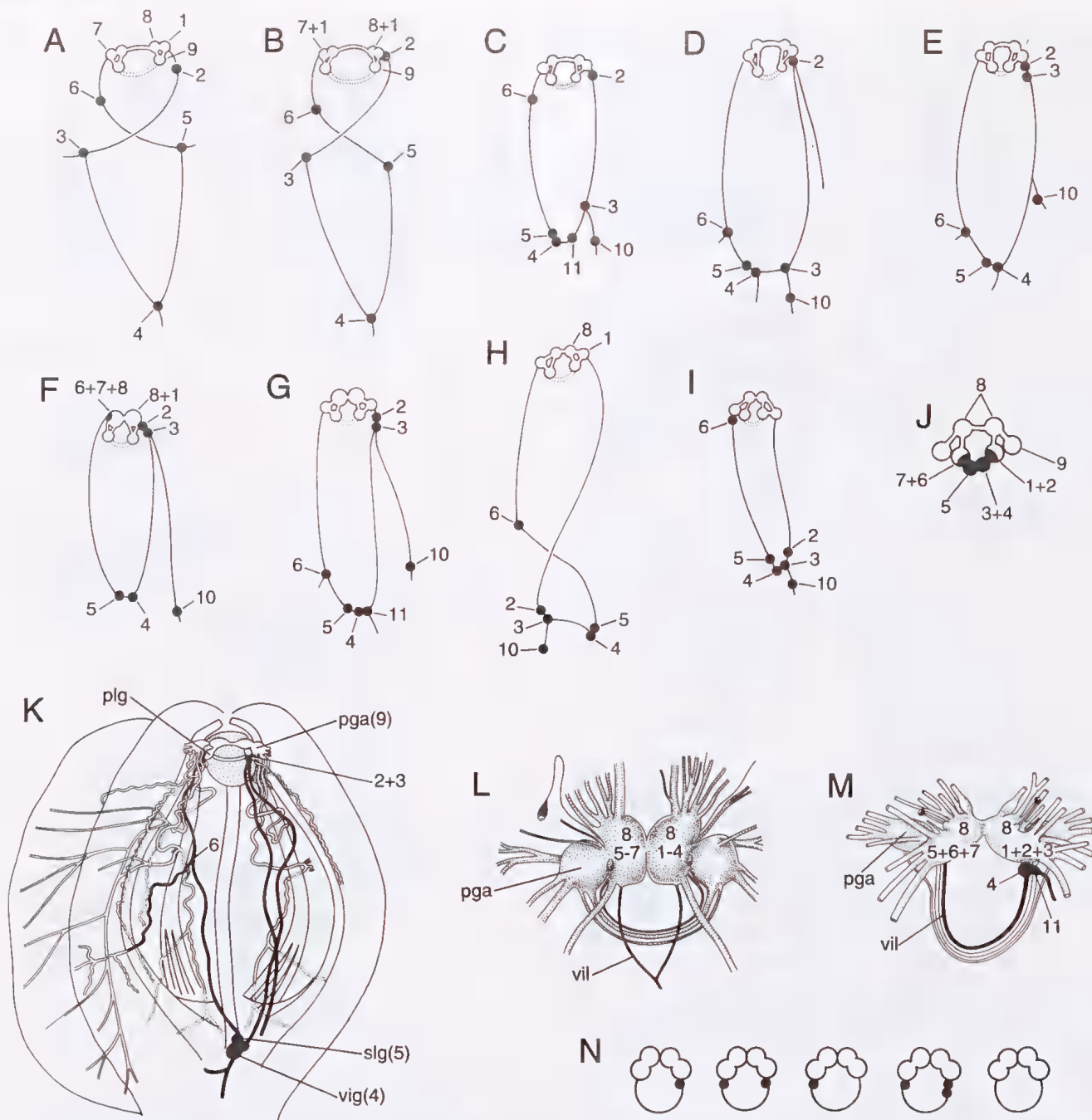


Figure 16.16 Opisthobranch nervous systems. In all figures the visceral loop and associated ganglia are shown in solid black. A–J, semi-diagrammatic representation of variation in the circumoesophageal nerve ring and visceral loop: A, *Acteon* (Acteonidae); B, *Pupa* (Acteonidae); C, *Haminoea* (Haminoeidae); D, *Philine auriformis* (Philineidae); E, *Philine powelli*; F, *Phanerophthalmus* (Smaragdineidae); G, family Aglajidae; H, *Akera* (Akeridae); I, *Aplysia* (Aplysiidae); J, *Notarchus* (Notarchidae). Note the retention of the 'streptoneuran' figure of eight loop in the primitive bullomorphs *Acteon* and *Pupa*, and the aplysiomorph *Akera*, which is lost in most other cephalaspideans and aplysiomorphs. *Notarchus* shows a great ganglionic concentration and loss of the visceral loop which mirrors the cephalisation found in the nudibranchs (see L, M). K, *Chelidonura electra* (Aglajidae) showing the major nerves and ganglia in situ. L, *Marionia blainvillea* (Tritoniidae), central nervous system showing the visceral loop reduced to a thin nerve loop and all the associated ganglia incorporated into a pair of large cerebropleural ganglia. M, N, *Austroderis kerguelensis* (Dorididae): M, circumoesophageal nerve ring showing the concentration of ganglia; N, variation in the number of visceral ganglia which actually coalesce with the cerebropleural mass in different specimens. 1, 7, pleural ganglia; 2, 6, parietal ganglia; 3, supra-oesophageal ganglion; 4, visceral ganglion; 5, suboesophageal ganglion; 8, cerebral ganglion; 9, pedal ganglia; 10, osphradial ganglion; 11, genital ganglion. pga, pedal ganglion; plg, pleural ganglion; slg, suboesophageal ganglion; vig, visceral ganglion; vil, visceral loop. (A, H, I, after Guiart 1901; B, after Rudman 1972b; C, after Rudman 1971a; D, E, after Rudman 1972f; F, after Rudman 1972g; G, K, after Rudman 1974; J, after Vayssi re 1885; L, Vayssi re 1902; M, N, after W gele 1990b) [R. Plant]

pedal commissure to the other pedal ganglion. A third ganglion on each side lies behind the other two. Each pleural ganglion is connected to both the cerebral and pedal ganglia on its side by separate commissures (Fig. 16.16). From each pleural ganglion a large nerve cord runs back to the visceral ganglion which lies on the floor at the posterior end of the body cavity. The link from one pleural ganglion to the other via the visceral ganglion is known as the 'visceral nerve loop'. It is a simple loop in euthyneurous systems, but forms a figure eight in *Acteon* and streptoneurous forms. Associated with this visceral loop are two other ganglia on each side, the parietal and oesophageal. These are often separate,

but sometimes the parietal and oesophageal ganglia on one may be fused together, the parietal may be fused with the pleural or the oesophageal fused with the visceral. When fusion occurs it seldom occurs symmetrically on both sides of the visceral loop.

The degree of ganglionic fusion varies in different groups and sometimes within a genus (see *Philine*, Rudman 1972f). Unfortunately, there is much confusion in the literature concerning the names of the visceral loop ganglia. The parietal ganglia are often named the pallial or accessory ganglia, while the oesophageal ganglia have been called the intestinal ganglia. As discussed by Haszprunar (1988), 'euthyneury' is not always a

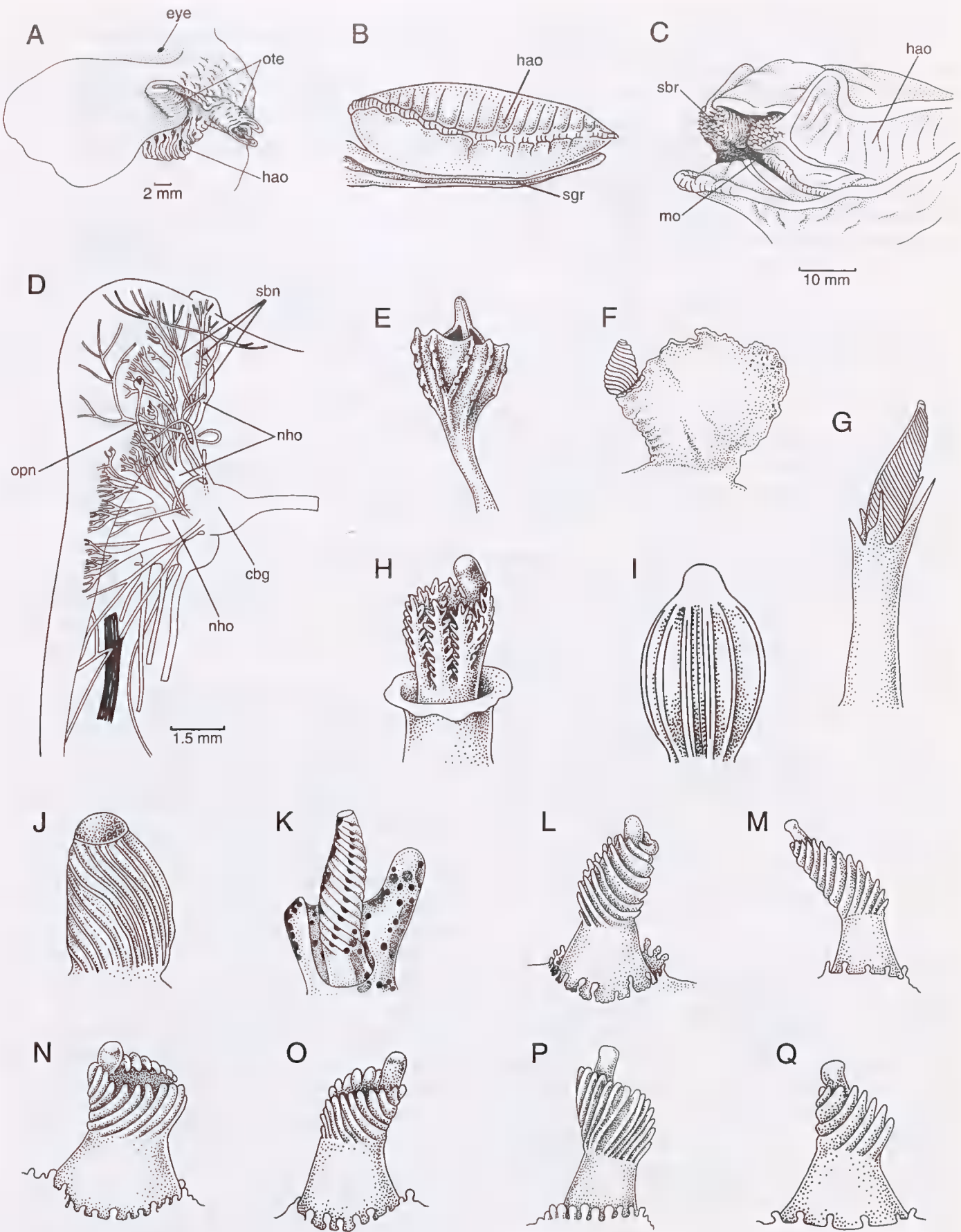


Figure 16.17 Opisthobranch sensory structures. A, *Hydatina pysis* (Hydatinidae), right side of head shield showing the paired cephalic tentacles and the large folded Hancock's organ. B, *Haminoea cymbalum* (Haminoeidae), the right Hancock's organ. C, *Chelidonura inornata* (Aglajidae), antero-lateral view of the head showing the left Hancock's organ and 'sensory bristles' typical of aglajids. D, *Aglaja inermis* (Aglajidae), showing the nerves to the anterior right side of the head, including those which innervate the Hancock's organ. E–Q, chemosensory rhinophores of nudibranchs. E–H, Dendronotoidea: E, *Hancockia californica* (Hancockiidae); F, *Melibe leporina* (Tethydidae); G, *Lomanotus genei* (Lomanotidae); H, *Tritonia gombergi* (Tritoniidae). I, J, Euarminoidea: I, *Dermatobranchus fortunatus* (Arminidae); J, *Armina punctilucens* (Arminidae). K, Anadoridoidea: *Thecacera pennigera* (Polyceridae). L–Q, Eudoridoidea – range of shapes within the genus *Rostanga* (Dorididae): L, *Rostanga arbutus*; M, *Rostanga bifurcata*; N, *Rostanga australis*; O, *Rostanga calumus*; P, *Rostanga muscula*; Q, *Rostanga bassia*. cbg, cerebral ganglion; eye, eye; hao, Hancock's organ; mo, mouth; nho, nerves to Hancock's organ; opn, optic nerve; ote, oral tentacles; sbn, nerves to sensory bristles; sbr, sensory bristles; sgr, seminal groove. (A, after Rudman 1972a; B, after Rudman 1971a; C, D, after Rudman 1974; E, after MacFarland 1923; F, J, after Bergh 1870; G, after Eliot 1910; H, K, after Alder & Hancock 1855; I, after Bergh 1888b; L–Q, after Rudman & Avern 1989) [R. Plant]

16. OPISTHOBRANCHIA

good diagnostic character of the Euthyneura (Opisthobranchia and Pulmonata). However, the presence of the two parietal ganglia is, according to Haszprunar. The 'pentaganglionate' state of the visceral loop (the visceral ganglion and pairs of parietal and oesophageal ganglia) is unique to the Euthyneura.

The anterior cerebropleuropedal ring is often known as the circumoesophageal ring for it is found at the rear of the buccal bulb, or pharynx, around the oesophagus in most nudibranchs, anaspideans and sacoglossans. In the Notaspidea, it may be posterior to the buccal bulb (*Tylodina*; see MacFarland 1966) or around the anterior end of the buccal bulb (*Pleurobranchus*, see Thompson 1976). Most cephalaspideans have the ring around the anterior end of the buccal bulb, although in runcinids the ring is around the oesophagus (Rudman 1971b).

The paired eyes of opisthobranchs are usually found sub-epidermally, in many species close to, or adhering to, the circumoesophageal nerve ring. Meisenheimer (1905) described much reduced eyes at the tips of the cephalic tentacles in pteropods, but van der Spoel (1985) considered the 'eyes' to be an aggregation of ganglia rather than light receptors. The opisthobranch eye is simple. The vesicle wall consists of a thin corneal section nearest the epidermal layer of the body and a thickened and darkly pigmented retina on the opposite side. There is a spherical, or reasonably symmetrical lens in the cavity of the eye vesicle. These eyes register light and shade but there is no evidence to suggest that they can distinguish shapes or colours.

All opisthobranchs have a pair of statocysts. These are innervated from the cerebral ganglion but are usually situated against the pedal ganglion. The statocyst is a hollow sphere containing one large statolith or a number of smaller calcareous statoconia (Franc 1968).

Primitive shelled opisthobranchs have a sensory osphradium in the mantle cavity just anterior to the gill. It differs structurally from those of most caenogastropods (Haszprunar 1985a, 1985b), but is similar to those of pyramidellids and architectonicids. It is reported to occur in primitive cephalaspideans with a forward opening mantle cavity, such as *Acteon* (Fretter & Graham 1954), *Pupa*, *Hydatina* (Rudman 1972a, 1972b), *Haminoea* (Rudman 1971a), and also the anaspidean, *Aplysia* (Kandel 1979), and the sacoglossans, *Ascobulla* and *Lobiger* (Marcus, Ev. & Marcus, Er. 1956a; Gonor 1961a). It is reported by MacFarland (1966) from the notaspidean *Tylodina*. The fine structure of the osphradium suggests that it is chemosensory in function (Haszprunar 1985a, 1985b). Croll (1985) suggested that in *Aplysia* it assists in the regulation of respiration by detecting changes in the pH of sea water.

Hancock's organs are another feature of the sensory system of the shelled opisthobranchs. These are sensory regions on each side of the head usually in the groove between the foot and the dorsal head shield. They are present in most cephalaspideans. They are said to be absent in *Acteon* (Fretter & Graham 1962; Hyman 1967; Schmekel 1985), but are clearly present in the acteonid genera *Pupa* and *Maxacteon* (Rudman 1972b) and present and elaborated into a large folded structure in *Bullina*, *Micromelo* and *Hydatina* (Fig. 16.17A) (Rudman 1972a, 1972i). They are also present throughout the Haminoeidae (Fig. 16.17B) (Rudman 1971a, 1972g), and the carnivorous Scaphandridae, Philinidae and Aglajidae (Fig. 16.17C), the primitive genus *Diaphana* (see Fretter & Graham 1962) and the shelled sacoglossans *Ascobulla*, *Volvatella* and *Lobiger* (Marcus, Ev. & Marcus, Er. 1956a; Gonor 1961a; Baba 1966).

Unique sensory structures have been described in the Philinidae and the Aglajidae. Two highly innervated brown patches on each side of the mouth of *Philine* are considered to be sensory (Brown 1934; Rudman 1972e, 1972f) and all genera of the Aglajidae have a large mound on each side of the mouth which bears a collection of retractile bristles, possibly compound cilia (Fig. 16.17C). These are highly innervated by connectives from the cerebral ganglion (Fig. 16.17D) and are most probably used to follow the mucous trail of their prey.

In many opisthobranch groups, head tentacles are important sensory structures although the homologies of head tentacles of different groups, and their function, need further study. Anaspideans have two pairs of tentacles which are very similar histologically. They are enrolled, tubular structures and although the posterior pair are known as 'rhinophores' both they and the anterior tentacles have been shown to be involved in chemoreception in the well-studied *Aplysia californica* (see Kandel 1979).

In sacoglossans, only an anterior pair of either enrolled or solid 'oral' tentacles are present. They are called 'rhinophores', but their function seems unknown. The notaspidean genera *Umbraculum* and *Tylodina* have a pair of enrolled oral tentacles; others in this group have an oral veil which is produced into a grooved tentacle on each edge. All notaspideans have a pair of enrolled 'rhinophores' in the anterior mid-line which are presumed to have a chemosensory function. The oral veil and tentacles are reported to be sensitive to tactile stimuli (Willan 1987a).

The specialisation of the posterior pair of head tentacles to form chemosensory organs is most highly developed among nudibranchs. These tentacles, known as rhinophores, range from simple tapering rods to elaborate, lamellate or tuberculate organs (Fig. 16.17E–Q) and are usually capable of rapid retraction into protective pockets when touched.

Reproduction

All opisthobranchs are hermaphroditic, sperm being exchanged by both partners during copulation. In some species the testis matures first (protandrous), but it is assumed that their sperm is stored either before or after copulation until the eggs are mature (Rudman 1972b).

The anatomy of the reproductive system is extremely diverse (Fig. 16.18). Authors of various review articles (Ghiselin 1966; Beeman 1977; Gosliner 1980; Schmekel 1985) have attempted to collate the data from taxonomic papers and to provide an overall synthesis and evolutionary perspective. The reproductive system consists of an inner section of mesodermal origin containing the gonad (ovotestis) and part of the gonoduct which may widen into an ampulla which stores sperm produced in the testis (endogenous sperm). The rest of the reproductive organs are ectodermal in origin and include a short post-ampullar section of the gonoduct and up to three ducts which carry eggs and endogenous sperm out and exogenous sperm in during copulation and egg-laying.

Most reviews emphasise the importance of the number of ectodermally derived gonoducts in discussing opisthobranch evolution. If there is only one tube the system is termed monaulic; diallic and triaulic systems have two and three tubes, respectively (see Chapter 14). In the triaulic forms (Fig. 16.18L, M), one duct carries endogenous sperm out to the penis (vas deferens), one carries exogenous sperm in to fertilise the endogenous eggs (vagina), and the third carries fertilised eggs out (oviduct). If there are only two ducts the oviduct and vagina may be combined while the vas deferens remains separate (androdiallic), or the two sperm ducts may be combined, with the oviduct remaining separate (oodiallic).

All opisthobranch reproductive systems have evolved systems which separate endogenous eggs and sperm from exogenous sperm, until cross-fertilisation can be achieved, thus preventing self-fertilisation. In functional terms, therefore, it is of minor importance whether there are one, two or three ectodermal ducts. However, the number of ducts has been considered of great phylogenetic importance. Many authors have considered the monaulic system to be the most primitive state (Ghiselin 1966; Beeman 1977; Gosliner 1980; Schmekel 1985) and while this may prove to be so one must realise that, as with other opisthobranch organ systems, much parallel evolution has occurred in the group. It is possible that secondary monaulism, and dialulism, has occurred more than once.

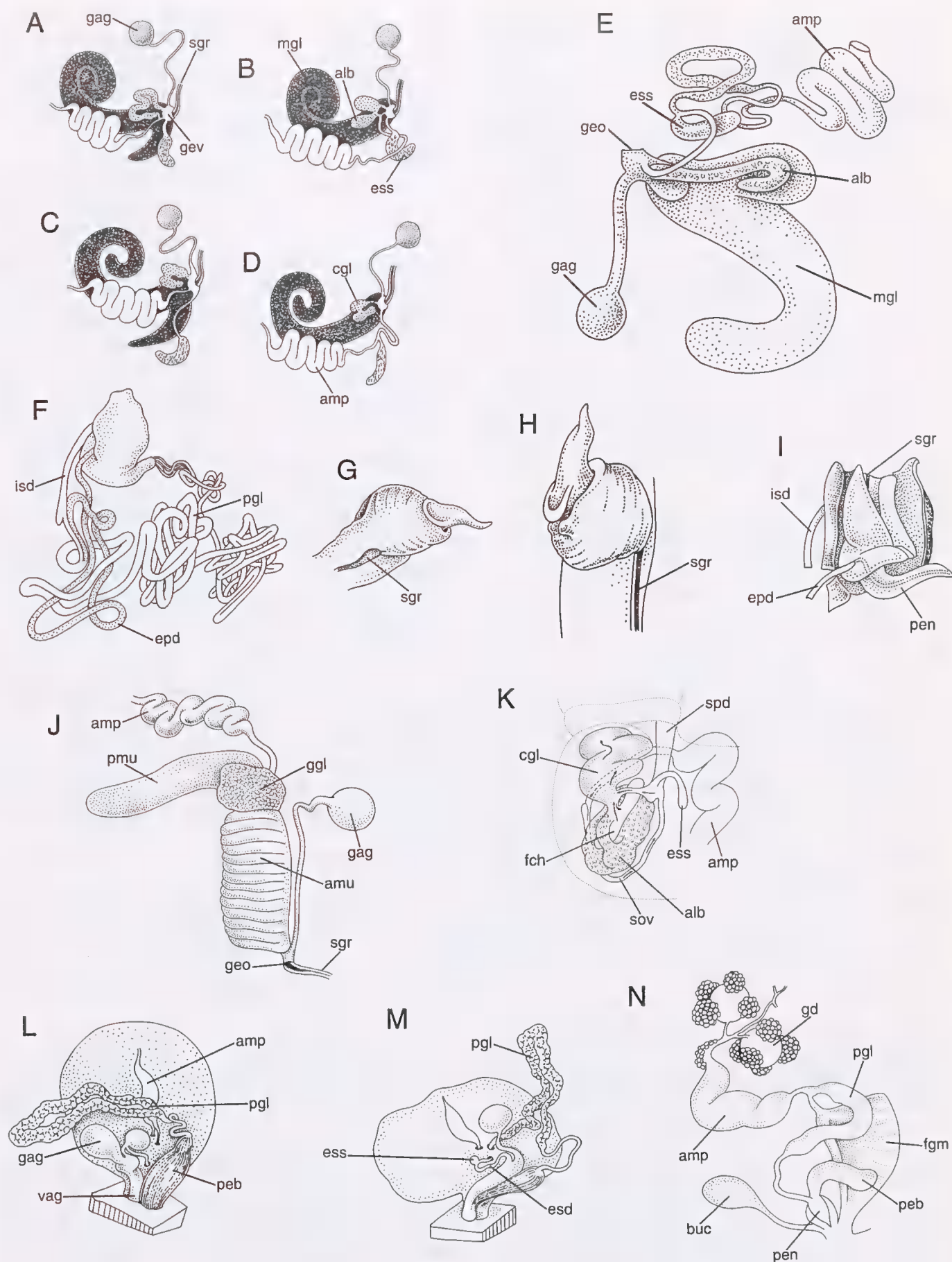


Figure 16.18 Opisthobranch reproductive systems. A–D, showing variation in the aglajid Cephalaspidea from an oodialic system in *Melanochlamys* (A) and *Chelidonura* (B), to a monaulic system in *Philinopsis* (C) and usually in *Aglaja* (D). E–I, *Philine auriformis* (Philinidae): E, monaulic system; F–I, penis and associated prostate gland connected by external seminal groove to reproductive opening. J, K, *Haminoea zelandiae* (Haminoeidae): J, monaulic system; K, albumen-capsule gland and the passage of eggs, indicated by arrows. L, M, triaulic system of the dorid nudibranchs *Chromodoris ambiguus* (L) and *Chromodoris alternata* (M) (Chromodorididae). N, triaulic system of the aeolid nudibranch *Cuthona kuiteri* (Tergipedidae). alb, albumen gland; amp, ampulla; amu, anterior mucous gland; buc, bursa copulatrix; cgl, capsule gland; epd, ejaculatory duct; esd, exogenous sperm duct; ess, exogenous sperm sac; fch, fertilisation chamber; fgm, female gland mass; gag, gametolytic sac; gd, gonad; geo, genital opening; gev, genital vestibule; ggl, genital gland mass; isd, incurrent sperm duct; mgl, mucous gland; peb, penial bulb; pen, penis; pgl, prostate gland; pmu, posterior mucous gland; sgr, external seminal groove; sov, spermoviduct; spd, sperm duct; vag, vagina. (A–D, after Rudman 1974; E–I, after Rudman 1972f; J, K, after Rudman 1971a; L, M, after Rudman 1987b; N, after Rudman 1981a) [R. Plant]

There are clearly many anomalies. In the 'most primitive' of the cephalaspideans, *Acteon*, *Pupa*, *Hydatina* and *Bullina* (Fretter & Graham 1954; Rudman 1972a, 1972b, 1972i), androdiaulic systems are found, whereas in the Philinoidea the 'primitive' *Cylichna* and the 'advanced' *Chelidonura* (Fig. 16.18A–D) have oodiaulic systems, though most other philinoideans (Fig. 16.18E–H) have a monaulic system. The Retusidae, Haminoeidae (Fig. 16.18J, K), Runcinoidea and Anaspidea are also monaulic (Rudman 1978). Whatever the system in the 'ancestral opisthobranch', it appears that in some advanced cephalaspideans a secondarily monaulic system has evolved by the shortening of the pallial gonoducts, associated with the degeneration of the mantle cavity.

Within the Notaspidea, *Tylodina* and *Umbraculum* have a monaulic system while the more advanced genera have either an androdiaulic or triaulic system (Willan 1987a). Similarly, nudibranchs are either androdiaulic or triaulic.

Various glandular regions have evolved in the reproductive system, as have also two sperm sacs. In the following account, the vas deferens, vagina and oviduct are considered to be functionally separate ducts, but the principles apply equally to a monaulic system where the ducts appear physically combined or to triaulic systems where the ducts are physically, as well as functionally, separate.

Usually a prostate gland is associated with the vas deferens or penis. Sometimes it lines part of the vas deferens and sometimes it is a separate sac or diverticulum opening into either the vas deferens or the penis. In some opisthobranch families, the penis opens at the anterior end of the body on the right side of the head. In these, an external seminal groove links the genital opening midway down the right side of the body to the penial sac (Fig. 16.18G, H, I; Haminoeidae, Aglajidae, Philinidae, Anaspidea). In other families, there is an internal duct (Acteonidae, Hydatinidae). The penis is a large external organ, lying folded in the mantle cavity in the Acteonidae and related families (Rudman 1972a, 1972b, 1972i), but in most opisthobranchs it is a retractile muscular organ with an external seminal groove or an internal muscular ejaculatory duct. Sometimes it is armed with cuticular spines.

The vagina can lead to two sperm sacs, and is armed with spines in some species. The two sperm sacs are considered to have distinct functions; however, only one is present in some families. One is considered to collect exogenous sperm at, or soon after, copulation and to break down prostatic secretions and waste gametic products; this sac has variously been termed the bursa copulatrix, gametolytic gland and gametolytic sac (Fig. 16.18J, L, M). The second sperm sac, or seminal receptacle, is said to retain or store orientated exogenous sperm until the eggs are ready for fertilisation.

Large glands usually are associated with the oviduct. In most opisthobranchs, three main regions of the oviduct contribute to the egg and egg mass. The first produces an 'albumen' layer around the egg, and provides an extra-embryonic nutritive layer, largely comprising galactogen and protein (Ghiselin 1966; Sanders-Esser 1984); nudibranchs and notaspideans are said to lack this layer (Schmekel 1970, 1971), but Ghiselin (1966) suggested its presence in some dorids. In the second region, the egg is surrounded by a thin 'capsule' or 'membrane' produced by the capsule or membrane gland; the capsules are characteristically attached to each other by a narrow string (chalaza) of the same material. The major glandular mass, the mucous gland, produces the jelly-like egg masses so characteristic of the opisthobranchs (Fig. 16.19).

Extensive reviews on reproduction and embryology of opisthobranchs have been published recently (Beeman 1977; Hadfield & Switzer-Dunlap 1984). Some opisthobranchs, specifically anaspideans, are often found together in large numbers, considered by many authors to be breeding aggregations. There may, however, be another explanation. It is

possible that after favourable settlement of large numbers of larvae in a confined area and rapid growth to maturity, large populations of adults will be found in close proximity. Mature adult opisthobranchs in close proximity usually attempt to copulate. Whether large numbers of aplysiids found together and copulating should be considered a 'breeding aggregation' may be a matter of semantics.

Nevertheless, there is evidence to suggest that *Aplysia californica* can detect the odour of conspecifics (Audesirk & Audesirk 1977). It has been suggested that some other opisthobranchs find partners by following mucous trails (Kawaguti & Yamasu 1960, *Berthelinia limax*; Todd 1979, *Onchidoris bilamellata*). Considering the high food-specificity of many species, it is likely that most meet their partners through chance encounters during feeding. Little is known about aspects of behaviour such as courtship or long-term pairing, and most authors assume that most opisthobranchs mate with many partners during their lifetime. This is probably so, but some, for example, the corallivorous aeolids, *Phestilla lugubris* and *P. minor*, pair for an extended period, even to the extent of producing homing scars on the coral colony (Rudman 1981b).

Usually opisthobranchs copulate reciprocally in pairs. In most, the position of the genital openings on the anterior right side of the body requires the pair to position their two right sides in contact. Each partner inserts 'his' penis into the other's vagina and sperm are exchanged. Copulation can be brief, or last for up to 24 hours, as in the large dorid *Hexabranhus sanguineus* (Gohar & Soliman 1963). In some primitive opisthobranchs (anaspideans and cephalaspideans) in which the penis is at the anterior end of the body and the vagina more posterior, reciprocal 'head to tail' copulation is often replaced by a unilateral system where one partner acts as the male and the other solely as female. In aglajids, pairs are often found in which the 'male' partner approaches posteriorly and inserts its penis in the posteriorly directed vaginal opening, as described for *Melanochlamys* by Rudman (1972c). Species of *Aplysia* have often been reported to copulate unilaterally (Eales 1921). Such a method of copulation can lead to long chains of conspecifics mating together; the anteriormost animal acts only as female, the hindmost as male, and those between as both male and female (Eales 1921; Rudman 1972c).

In many sacoglossans, hypodermic insemination occurs. There is no vaginal opening and the 'male' injects the sperm into the 'female' after piercing 'her' body wall with the cuticular tip of 'his' penis. In some species, the sperm can be injected anywhere into the body cavity but in other species usually into a specific area of the body wall. Hypodermic impregnation allows both reciprocal copulation and the formation of chains of individuals (for example, in *Elysia maoria*) similar to that described above for aplysiids (Reid 1964).

Eggs of opisthobranch species vary greatly in diameter, from about 40–50 µm in some sacoglossans (Clark & Jensen 1981) to about 400 µm in the nudibranch *Cadlina laevis* and the cephalaspidean *Philine gibba* (Thompson 1967; Seager 1979). Although sacoglossans and anaspideans usually have relatively small eggs and nudibranchs show the greatest range in egg size (Hadfield & Switzer-Dunlap 1984), egg size is more closely correlated with form of larval development than with phylogeny. Eggs can be divided into three broad size groups: small eggs (30–170 µm) usually develop into planktotrophic larvae; medium-sized eggs (110–250 µm) develop into lecithotrophic larvae; and large eggs (greater than 200 µm) usually have a suppressed larval stage leading to direct development (Thompson 1967). Also associated with egg size is the number of eggs laid: the smaller the eggs the greater the number produced. Developmental strategies vary widely, even within the same genus as has been shown recently (for example, Rudman & Avern 1989) for species of the nudibranch genus *Rostanga* in Australia and New Zealand.

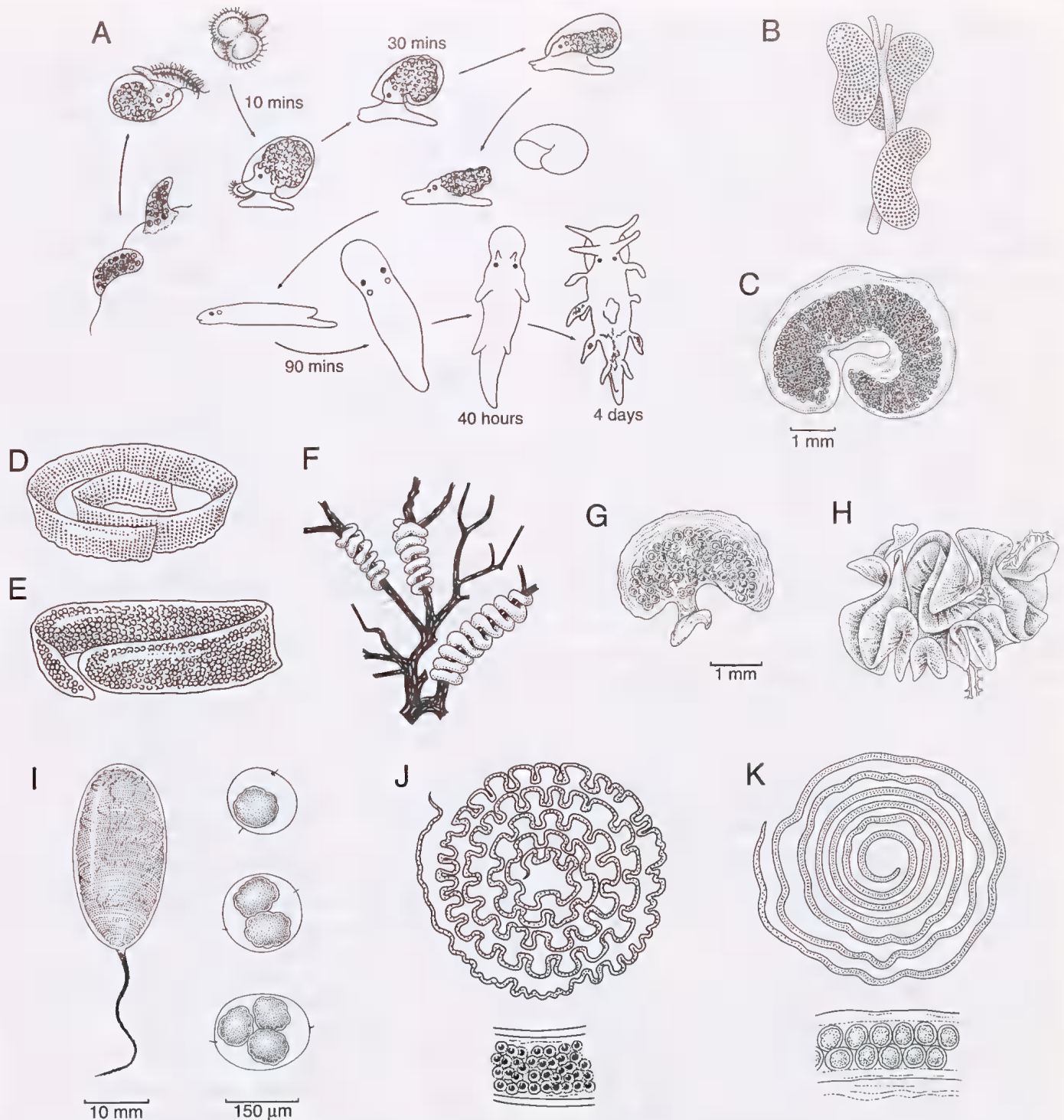


Figure 16.19 Opisthobranch developmental stages and egg masses. **A**, developmental stages in the corallivorous aeolid, *Cuthona poritophages* (Tergipediidae), showing the rapid larval metamorphosis. **B–K**, egg masses: **B**, *Haminoea zelandiae* (Haminoeidae); **C**, *Stiliger boodlee* (Limapontiidae); **D**, *Goniodoris castanea* (Goniodorididae); **E**, *Hypselodoris festiva* (Chromodorididae); **F**, *Protaeolidiella juliae* (Aeolidiidae); **G**, *Dermatobranchus striatellus* (Arminidae); **H**, *Melibe vexillifera* (Tethydidae); **I**, *Philine japonica* (Philinidae), showing capsules with one (usual), and two to three eggs; **J**, *Sakuraeolis enosimensis* (Glaucidae); **K**, *Favorinus japonicus* (Glaucidae). (**A**, after Rudman 1979; **B**, after Rudman 1971a; **C**, after Hamatani 1960; **D**, **E**, **H**, **J**, **K**, after Baba, Hamatani & Hisai 1956; **F**, after Rudman 1990b; **G**, after Hamatani 1967; **I**, after Hamatani 1961)

Opisthobranch eggs are usually enclosed individually in a transparent capsule, but Lalli & Wells (1973) reported that the thecosome *Limacina inflata* lacks a capsule and Rudman (1972b) described a similar observation for the bullomorph *Pupa kirki*. Each egg capsule, when present, is attached to the previous one and the next one by a twisted thread (chalaza) of the capsule material. The string of eggs is usually twisted in a spiral coil within a jelly-like mucoid egg mass. The opisthobranch egg mass has many forms (Fig. 16.19B–K) but they can be categorised as a few basic shapes, described by Hurst (1967) in a review of North American species. Many individual descriptions of egg masses can be found in the taxonomic literature; Smith, B.J., Black & Shepherd (1989) recently described egg masses of a number of southern Australian opisthobranchs.

Egg masses assume one of three basic shapes. In many burrowing cephalaspideans the egg mass is a globular gelatinous bag anchored in the substratum by a string (*Philine*, Aglajidae) (Fig. 16.19I). In others the gelatinous bag is more cylindrical and is attached along one side (*Haminoea*) (Fig. 16.19B). The second shape is a cylindrical tube in which the eggs are again arranged in a coil. In most anaspideans, the cylinder is long and narrow and forms a large tangled mass attached to plant growth or rocks, but in a few genera (*Dolabrifer*, *Petalifera*) it lies as a tight folded string flat against the substratum. Sacoglossans may have this type of string as do many aeolid nudibranchs. In some species, especially in small aeolids, the cylinder is very short and forms a small curved sac (Fig. 16.19A) attached along one side to the substratum (*Cuthona poritophages* Rudman 1979;

Cuthona kuiteri Rudman 1981a). The most recognisable egg mass is the flattened ribbon (Fig. 16.19D, E) produced by many nudibranchs and notaspideans. It is also found in some cephalaspideans (Fig. 16.19H) (*Hydatina*, *Bullina*). Usually the ribbon is attached along one edge and arranged in a spiral as found in many dorids. In species that live on branching or narrow substrata, such as hydroids or plants, the ribbon may be attached along or around the 'branch' (Fig. 16.19F). Often the free edge of the ribbon is longer than the attached edge and is thrown into a series of sinuous folds.

There are of course many variations on these three basic shapes and in any one genus two or more different types of egg mass are found. Some species in the nudibranch genus *Rostanga* have the typically flattened dorid ribbon arranged in a spiral while others have a short cylindrical mass attached to the substratum along one side (Rudman & Avern 1989). Among pelagic forms unable to attach eggs to a substratum, unique adaptations have evolved. Most thecosomes that have been studied release floating egg masses into the water, and the eggs develop into planktotrophic veligers (Lalli & Gilmer 1989). However, young larvae of *Limacina inflata* are brooded in the mantle cavity until a later veliger stage is reached (Lalli & Wells 1978). Gymnosomes produce a large spherical mucoid egg mass; that of *Clione limacina* can contain up to 2000 eggs (Lalli & Gilmer 1989). Brooding has been reported in one species, *Hydromyles globulosa* (Martoja 1965). The pelagic aeolids, *Glaucus* and *Glaucilla*, also produce a floating egg mass, which comprises a short mucoid tube containing an uncoiled row of 10 to 30 eggs.

Oviparity is the rule in most opisthobranchs. Apart from the examples of brooding described above for pteropods, Rudman's (1972b) record of brooding of non-capsulated larvae in the cephalaspidean *Pupa kirki* is the only recorded example of development not occurring totally outside the body. There is little evidence of parental care of the egg mass after it is deposited. Only the aeolid *Pteraeolidia ianthina* (Pl. 4) has been observed apparently guarding egg masses, either individually or in aggregations (Rose & Hoegh-Guldberg 1982). Possibly because it gains some nutrition from symbiotic zooxanthellae (Rudman 1982a), this species is able to remain with the eggs for some time without feeding, and thus to protect them from predators with its nematocysts. Developmental and larval biology are discussed elsewhere in this introduction.

Sperm morphology has been reviewed in detail (Thompson 1973a; Beeman 1977; Hadfield & Switzer-Dunlap 1984; Healy & Willan 1991a; Healy 1993). Opisthobranch sperm are characterised by their helical shape. The 'body' of the sperm is the long muscular flagellum and the nucleus consists of an anterior 'head' region and an elongate thread that wraps itself in a spiral coil around the flagellum, sometimes down its entire length. Elongate mitochondrial threads also form spirals around the flagellum. There are two mitochondria in anaspideans, in nudibranchs one, and in the cephalaspidean *Acteon*, four have been observed.

Recent comparative studies on sperm ultrastructure in nudibranchs and other opisthobranchs have been reviewed by Healy & Willan (1991a). Although useful in confirming higher relationships among the Heterobranchia, many more species need to be examined before variations in sperm ultrastructure can be used confidently to interpret phylogenetic relationships.

In most opisthobranchs, the sperm are delivered directly to the partner during copulation. There are several reports of the presence of spermatophores in species from four orders—Cephalaspidea, Thecosomata, Acochlidia and Nudibranchia (Hadfield & Switzer-Dunlap 1984)—but little is known about spermatophores in opisthobranchs generally. In all species, the spermatophore is a small, thin-walled sac. In acochlidians, it attaches to the body wall of the copulatory partner and the sperm enters the recipient's haemocoel through the body wall without copulation. In other groups, the spermatophore is considered to enter through the genital aperture.

NATURAL HISTORY

In recent years, a number of major reviews of the ecology, life history and reproductive biology of opisthobranchs have been published, mainly on nudibranchs (Todd 1981, 1983; Hadfield & Switzer-Dunlap 1984). These reviews cover much of the relevant published work and indicate clearly that little is known about the basic biology of many opisthobranch groups. The following account uses some known examples to illustrate possible broad trends in opisthobranch natural history, but it would be unwise to interpret this to mean that we have a good knowledge of opisthobranch biology.

Most opisthobranchs live for less than a year, although the tropical aplysiid, *Dolabella auricularia*, has been reported to survive for six years in an aquarium (Hadfield & Switzer-Dunlap 1984) and the Antarctic cephalaspidean *Philine gibba*, lives up to four and a half years in nature (Seager 1979, 1982). At the other extreme are the many small species which can complete a life cycle in a few weeks. In northern temperate waters, the aeolid *Tenellia pallida* is reported to mature 14–21 days after hatching (Rasmussen 1944) and the dorid *Doridella obscura* reaches maturity in 26 days (Perron & Turner 1977). In tropical waters, the coral-eating aeolid, *Cuthona poritophages*, reaches maturity within three weeks of hatching (Rudman 1979).

It is clear that opisthobranch life cycles and developmental strategies are linked to the food speciality of the adults. Briefly, those species that feed on transient food organisms, such as short-lived hydroids, are usually small and have a short life cycle including very rapid embryonic development. Conversely, species which feed on large long-living colonies, such as sponges or alcyonarians, are often larger, and have longer life cycles and slower embryonic development. Often the food resource of these animals is also their home site and their site of oviposition. An animal that has adapted to a transient food supply needs not only to be able to reach maturity but also to be sure that the eggs it lays are going to survive until they hatch. Time, and timing, are often critical.

Of equal interest, and also intimately connected with adult food, are larval development and biology. There have been many reviews of larval biology, and various grades of larval development type and larval shell type have been proposed. Basically, there are three types of larval development, but there tends to be a continuum or at least an absence of clear delineation of types.

The most common form of development is planktotrophic; small, shelled veliger larvae develop in a benthic egg mass and then at hatching are released into the water column as free-swimming, algal-feeding veligers. After a period of up to 30 days in the plankton the larvae settle on a suitable substratum and metamorphose into small benthic slugs. In the second type of development, lecithotrophic veliger larvae are produced. These are normally non-feeding larvae which spend, at the most, only a few days in the plankton before settlement and metamorphosis. The third type is known as 'direct development' in which all larval development occurs in the egg capsule and a small benthic slug emerges at hatching.

Much of the confusion concerning terminology and supposed ability to change development type within a species applies to the area separating direct development and lecithotrophy, for there are two types of direct development. In one, the embryo develops directly into a benthic slug without going through a visible veliger stage in the capsule. In the second type, the embryo clearly develops in the capsule into a veliger larvae, but instead of hatching, undergoes metamorphosis in the capsule, then hatches as a benthic slug. While in ecological terms any time in the plankton is significant, in developmental terms the difference between lecithotrophy and this second type of 'direct development' is very slight.

Ecologically, developmental type and larval settlement strategy are vitally important. During larval life, most opisthobranchs are relatively mobile and so are able to find optimal places to live, feed

and breed. Many recent studies have shown that larvae can delay settlement and metamorphosis for some time after they are competent to do so, until the correct chemical stimulus is sensed. In all cases studied, the chemical stimulus has been related to the adult food. The presence of a free-swimming larval stage, whether planktotrophic or lecithotrophic, ensures both the wide distribution of offspring and at the same time the capability of locating food supplies on which to metamorphose and grow to maturity.

Great risks are involved in casting one's offspring into the sea to fend for themselves, and there is a correlation between the number of eggs produced and the developmental type. Planktotrophic developers, with the most 'risky' strategy, produce many small eggs, while direct developers with the least 'risk' produce a few large eggs. Lecithotrophs fall somewhere in between.

Species relying on transient food sources usually grow rapidly to maturity and produce many planktotrophic larvae; their adult food colonies may be widely spread. Most direct developers feed on large, relatively long-lived colonies with sufficient mass and continual growth to allow successive generations to live continuously nearby. Food colonies are not immortal and some dispersal must be achieved by adult crawling or chance dislodgment. Some lecithotrophs are able to maximise use of resources with some larvae dispersing by swimming away from the 'home' colony and others resettling where they emerged. For example, most larvae from one egg mass of the coral-feeding aeolid *Cuthona poritophages* settle and metamorphose within 10 minutes of hatching, if the coral mucus stimulus is present, while a few can remain free-swimming for some days (Fig. 16.19A; Rudman 1979). In a reef situation, this variation would ensure that most larvae settle on the home coral colony, or a nearby colony, while a few larvae are available for the riskier exercise of dispersal. The ecology of larval development and distribution strategies is a fascinating study in itself. Such work is still in its infancy but details of many individual species can be found in the reviews of Todd and Hadfield & Switzer-Dunlap mentioned above.

The diversity of opisthobranch shapes is matched by the diversity in diets. In fact, in many species, especially among nudibranchs, shape, colour, and dietary specialisation are clearly related (Pls 34.1, 35.8, 37.1). In earlier studies of opisthobranch evolution, it was considered that the development of the 'nudibranch' form from caenogastropod-like heavy-shelled primitive opisthobranchs could be mirrored in diet, with 'microphagous-browsing' acteonids being replaced by more specialised feeders as the ancestral 'nudibranch' was freed from the constraints of its shell (Morton 1958a).

We now know that all primitive cephalaspideans are specialised feeders. Within the Acteonidae, *Acteon tornatilis* feeds on the tubeworms *Owenia* and *Lanice* (Hurst 1965; Yonow 1989). *Pupa kirki* and *Maxacteon cratericulatus* feed on sabellid and cirratulid worms, respectively, and cirratulid worms have been reported from the stomachs of the related *Hydatina amplustre* and *H. physis* (Rudman 1972c). Burn & Bell (1974a, 1974b) showed that two species of *Retusa* from Victoria are specialist feeders on other infaunal animals. *Retusa pelyx* feeds on only six of 23 species of foraminiferans available, whereas *R. chrysoma* feeds on a wider number of foraminiferans and also eats juveniles of the pulmonate, *Salinator fragilis*.

As in many cephalaspideans, chitinous gizzard plates have evolved in retusids to crush hard-shelled prey. In the Scaphandridae and Philinidae, however, calcareous gizzard plates have evolved, which allow crushing of the much harder shells of bivalves (Fig. 16.14). Each species in the genus *Philine* has adapted to a specialised diet of one or a few species of bivalves (Rudman 1972i). These cephalaspideans are infaunal, drably coloured, with either a large external shell or a small internal shell. In contrast, the Aglajidae include both burrowing and surface dwellers. They are often brightly coloured, all have lost the gizzard plates and most no longer have a radula. They are specialised hunters, each genus feeding in a slightly different way. *Melanochlamys* feeds on polychaete worms, while *Philinopsis*,

Navanax and *Aglaja* feed on other cephalaspidean opisthobranchs, which they track down by following their mucous trails with special cephalic sensory bristles (Rudman 1972e; Gosliner 1980). Not all cephalaspideans are carnivores. The Haminoeidae, Smaragdiniellidae, Bullidae and the closely related runcinoideans are all herbivores and grind their food with chitinous gizzard plates (Rudman 1971b). Two other orders, the Anaspidea and Sacoglossa, are also herbivorous.

Aplysiids, or sea-hares, are usually large and are often well camouflaged when feeding. They are found throughout the world and many of the species are circumglobal in distribution. There are many accounts in the literature of waves of migratory aplysiids aggregating for breeding but recent studies suggest that the vast numbers sometimes found on beaches are accidental wash-ups, after storms, of dying post-breeding adults. Because of the ease with which they can be kept in aquaria, and the large size of their nerve ganglia, aplysiids have become important laboratory animals in the experimental study of behavioural physiology (Kandel 1979). They are well known for the ability of some species to expel a cloud of red or purple dye when disturbed. Nolen, Johnson, Kicklighter & Capo (1995) demonstrated experimentally that this 'ink' does deter predators. Some intertidal species of *Aplysia* feed on a progression of algal species as they grow to maturity, and change colour to match their food as they grow. Others, such as the tropical *Stylocheilus*, feed on the cyanobacteria growing around intertidal pools on soft shores. The larvae settle on the shore and the young grow rapidly to form aggregations of adults, which mate and then die in a few weeks.

The other herbivorous group, the Sacoglossa, shows remarkable diversity in shape, ranging from the snail-like shelled *Ascobulla* and the bivalved *Julia* to the nudibranch-like *Stiliger* and *Polybranchia*. Despite the many shapes, diet and gut morphology are extremely uniform. In almost all genera, the radula has a single tooth in each row; *Olea* species are the exception with the radula vestigial. The individual teeth are sharp knife-like blades which are used to pierce the algal cells upon which these animals feed so that the cell sap can be sucked out.

A remarkable symbiosis has evolved in this order. Some sacoglossans are able to retain live plastids from the algae they ingest, in specialised ducts of the digestive system. Clark, Jensen & Stirts (1990) termed this association 'kleptoplasty' (derived from the Greek 'kleptos' = to steal). In the most highly specialised of these symbioses, plastids are retained alive and the photosynthetic products that they produce leave the plastid, becoming part of the sacoglossan's energy supply. Much physiological work has been undertaken worldwide to investigate this relationship; it has been summarised by Brandley (1984) in his study of *Elysia* cf. *furvacauda* in Botany Bay, Sydney. This species was shown to change its algal food seasonally and retain different functional plastids at different times of the year. It was found on green, red and brown algae and although no brown plastids were found, two types of chloroplast and one rhodoplast were found. This suggests that the notion that sacoglossans are restricted to one algal food type may, at least in some cases, be incorrect.

Not all sacoglossans have symbiotic plastids in their tissues. The symbiosis evolved in parallel with the change in body shape from the 'primitive' shelled forms, such as *Ascobulla*, which do not retain chloroplasts, to the 'nudibranch' unshelled forms such as *Elysia* and *Stiliger*, which do. There is a functional connection, for if plastids are to be kept alive and photosynthesising then they must be retained, as in a plant, in a leaf-like light-collecting structure. The cerata and flattened parapodia of many 'nudibranchiate' sacoglossans form the 'leaves' that these plant-like animals need to retain healthy plastids. As well as providing extra food resources for the sacoglossan, the incorporation of plastids of the same type as the alga on which the slug is sitting, means that the slug is effectively identical in colour to its substratum.

In the Notaspidea, *Umbraculum* and the primitive *Tylodina*, both recognisable by their large dorsal limpet-like shells, feed specifically on sponges of the class Demospongiae (Willan 1984).

16. OPISTHOBRANCHIA

The more primitive of the 'nudibranch' pleurobranchs, which still have a small internal shell, such as *Berthella*, also feed exclusively on sponges of the Demospongiae. *Berthellina citrina*, found throughout the Indo-West Pacific, and in Australia and New Zealand, feeds on a wide variety of sponges and is reported from Hawaii to feed on the hard corals, *Tubastrea*, *Porites*, and *Leptastrea* as well (Bertsch & Johnson 1981).

The biology of the large tropical species of *Pleurobranchus* has not been well studied but the available information suggests that this genus feeds exclusively on solitary and compound ascidians. The most advanced pleurobranch genus, *Pleurobranchaea*, is represented in Australia by *P. maculata*. Species of this genus are well known as voracious carnivores, eating a wide range of invertebrates but ignoring sponges and ascidians. In New Zealand, *Pleurobranchaea maculata* feeds on sea anemones, errant polychaetes and some molluscs (Willan & Morton 1984). Other authors have noted that in captivity species of *Pleurobranchaea* can be fed on raw meat, squid, fish, other opisthobranchs, and even smaller individuals of their own species.

The widest diversity of feeding type occurs among the carnivorous Nudibranchia. Within the Arminina, both cnidarians and bryozoans are utilised as food. Species of *Armina* are burrowers which emerge at night to feed on sea-pens (Pennatulaceans). Little is known of the feeding habits of the numerous, often intertidal, species of the related *Dermatobranchus* (Pl. 35.1), but unpublished observations from Australia and Hong Kong show that at least some species feed on alcyonarian soft corals. Two armininans from tropical Australia and elsewhere in the Indo-West Pacific are so unusual morphologically that each is placed in its own family. One of these, *Pinufius rebus*, is an obligate feeder on the scleractinian coral *Porites*, and the other, *Doridomorpha gardineri*, is an obligate feeder on the alcyonarian blue coral, *Heliopora coerulea* (Rudman 1981b, 1982a). Of other armininans, zephyrinids and madrellids differ from armininids in having rows of cerata around the mantle edge. These aeolidiform armininans feed exclusively on encrusting colonial bryozoans, each species apparently preferring one or a few species of bryozoans. *Caldukia affinis* is commonly found on bryozoan colonies under intertidal rocks in temperate Australia, and the red *Madrella sanguinea*, found in both temperate and tropical waters, is well camouflaged on its similarly coloured bryozoan, *Mucropetraliella*.

Members of the Dendronotoidea, another nudibranch group, feed mostly on cnidarians. While some, especially tritoniids, appear to feed exclusively on alcyonarian soft corals, others such as the aeolidiform bornellids and dotoids, feed on colonial hydroids. Tethydids are exceptional, as all prey on small crustaceans that they catch in a massively enlarged oral hood.

Dorids also have a great diversity of diets. Phanerobranch dorids (superfamily Anadoridoidea) feed on a wide variety of invertebrates including bryozoans, ascidians, sponges, polychaete worms and other opisthobranchs. Usually each family specialises on one or a few types of food. All the cryptobranch dorids (superfamily Eudoridoidea) are sponge feeders, most species preying upon only one or a very few species of sponge.

Almost all aeolids feed on cnidarians, including hydroids, alcyonarian soft corals, scleractinian hard corals, sea anemones, zoantharians and, rarely, pelagic siphonophores. Some exceptions include *Favorinus* species which feed on mollusc eggs, *Calma* species which prey on fish eggs, and the sole species of *Fiona*, which feeds on goose-barnacles *Lepas* species.

Dietary innovations and modes of nutrition have clearly influenced opisthobranch evolution. Most species show a preference for a single food species, or group of species, which has led to close links between aspects of the natural history and morphology of the predator and the prey. This is most evident in sacoglossans and nudibranchs. Camouflage in the adult slugs, through resemblance to both the shape and colour of the food they eat, is a common phenomenon. A whole group of sacoglossan

species feeds on the tropical green algae *Caulerpa racemosa*, easily recognised by the arrangement of its thallus in large bubble-shaped grape-like bunches. Among the white root-like stolons can be found the primitive white *Ascobulla*, while in the green 'bunches of grapes' five to ten species can be found. All are similarly coloured, for their pigment is derived from the thallus contents of *Caulerpa*, and those with shells have shells of similar size to the 'bubbles' of the *Caulerpa*. In one species, the shell-less *Stiliger smaragdinus*, large bubble-shaped cerata mimic the *Caulerpa* 'bubbles' in size, shape and colour.

Colour derived from the food has been used commonly by nudibranchs for camouflage. In the cryptobranch dorid genus *Rostanga*, many species are red or orange, each coloured to match the colour of the sponge colony on which it feeds (Rudman & Avern 1989).

Colour camouflage has also been effected in nudibranchs, not from prey-produced pigment, but from algal symbionts or zooxanthellae, which are removed from the prey and retained in the nudibranch's body. In species such as *Pinufius rebus*, feeding on large, variably coloured colonies of the coral *Porites*, individuals match perfectly the background of the part of the colony on which they are feeding (Rudman 1981b, 1982a). The uptake of living algal symbionts from their cnidarian food has led to the development of a wide range of physiological and morphological adaptations which will be discussed later.

Other species have evolved colour patterns that mimic those of the food colony on which they live. The corambid dorids (suborder Doridina), which feed exclusively on the colonial bryozoan *Membranipora*, are a well-known example. The bryozoan colony forms a distinctive white network on the dark brown laminarian algae upon which it is often found. The corambids have a white reticulate pattern on their dorsal surfaces which accurately matches the white skeletal outline of the colony. Another example of colour camouflage produced directly by nudibranchs is found in the pelagic *Glaucus* species which float upside down in the ocean, feeding on siphonophores such as the blue-bottle, *Physalia*. The anatomically 'ventral' surface of *Glaucus*, which floats upwards, is dark blue, camouflaging the slug from flying predators, and its effective underside (true dorsum) is silver, camouflaging it against predation from below.

In the Chromodorididae there is another relationship between food specificity and colour (Rudman 1984a). Some species, such as the pink colour form of the south-eastern Australian *Noumea haliclona*, match perfectly the colour of the sponge on which they feed, and others, such as the southern Australian *Verconia verconis*, match their food sponge in both shape and colour. However, most chromodoridids are vividly coloured and presumably are easily seen by potential predators (Pls 35.4, 35.5, 37.3). In this family, defensive mantle glands, which occur in many nudibranchs as randomly spread small glands, are modified to form specially arranged arrays of large compound glands which contain anti-predatory or anti-feedant chemicals, removed intact from the sponge on which they feed. Most chromodoridid genera have a specific arrangement of these mantle glands (Fig. 16.20A) and although there is no direct evidence at present, it seems clear that the glands produce a powerful deterrent to potential predators. The remarkable colour patterns found in many chromodoridids are now thought to be warning colouration announcing the presence of the mantle glands. The geographic clustering of similar colour patterns also seems to be significant. In south-eastern Australia there are many species with a white background and red spots. Often there is a yellow border to the mantle. It seems likely that these groups of similarly coloured species represent either a single large group, or many small groups of mimics, all warning potential predators that pursuit of prey with the particular colour pattern is likely to result in a distasteful meal (Rudman 1991a).

Distasteful anti-feedant chemicals are not the only items of defence that nudibranchs can obtain from their food. Many aeolids are able to remove the nematocysts (stinging cells) from the cnidarians upon which they feed and store them undischarged in

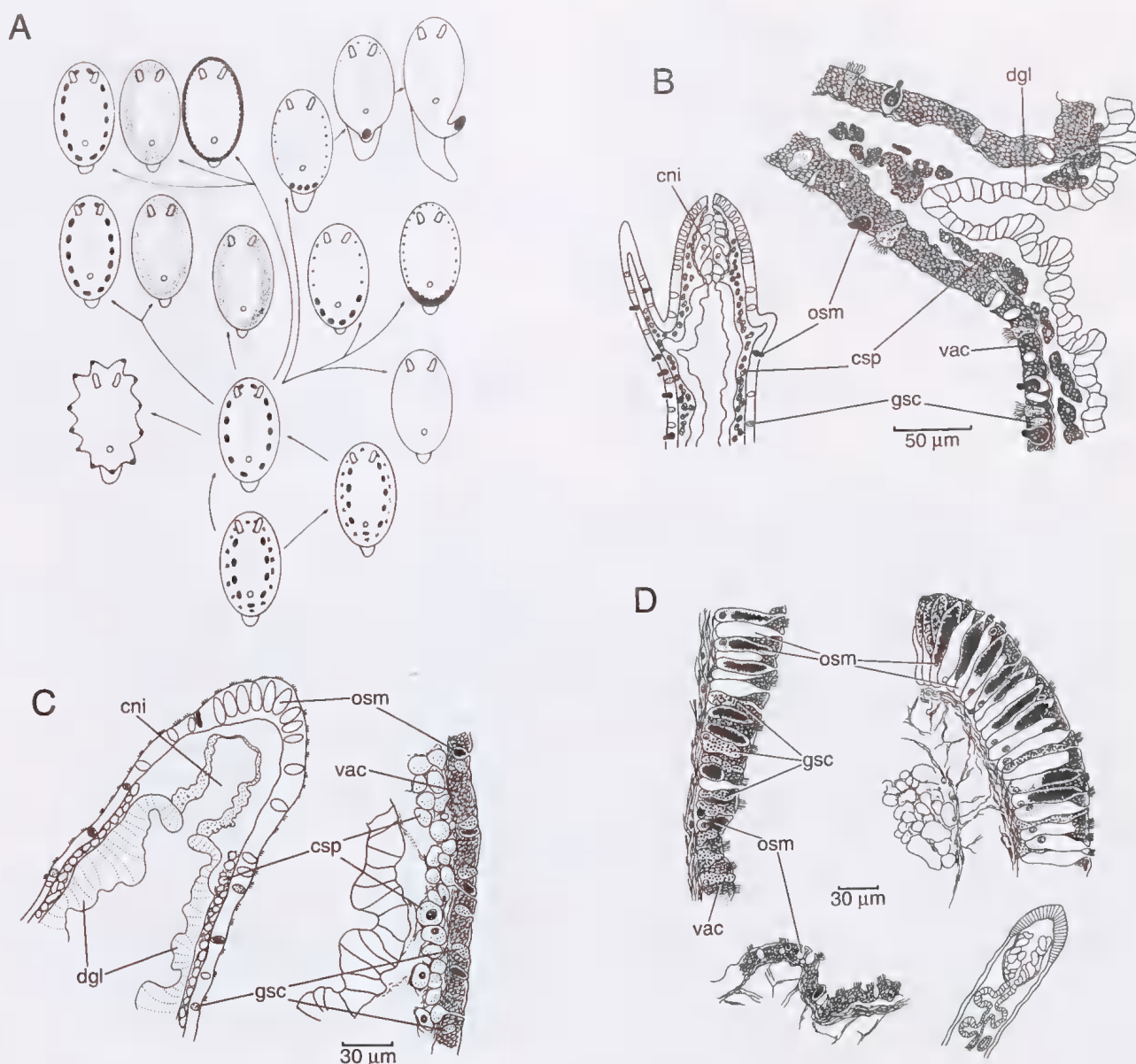


Figure 16.20 Opisthobranch defensive structures. **A**, the patterns of aggregation of defensive glands in the mantle of select genera in the dorid nudibranch family Chromodorididae. **B–D**, sections through the cerata showing the cellular structure and the 'rice grain' vacuoles packing the epithelial cells: **B**, *Cuthona kuiteri* (Tergipedidae), showing a typical aeolid ceratal structure with scattered epithelial glands and a large cnidosac containing cnidian nematocysts; **C**, *Cuthona poritophages*, a corallivorous species in which epithelial glands replace the apparently functionless cnidosac; **D**, *Phestilla lugubris* (Tergipedidae, a corallivorous species showing the massive development of defensive epithelial glands at the ceratal tip and the absent/degenerative cnidosac. **cni**, cnidosac; **csp**, cellule speciale; **dgl**, digestive gland; **gsc**, granular secretory cell; **osm**, osmiophil gland cell; **vac**, 'rice grain' vacuoles. (**A**, after Rudman 1984a; **B**, after Rudman 1981a; **C, D**, after Rudman 1971b) [A, D. Wahl; B–D, R. Plant]

sacs at the tips of their cerata (Fig. 16.20B). When disturbed, the aeolids are able to discharge these nematocysts from their cnidosacs to deter predators. In some aeolid species, the slug vigorously waves its cerata in an aggressive stance (Rudman 1980). The ability of aeolids to use the colour, shape and nematocysts of their prey for defence is epitomised by the Australian *Cuthona kuiteri*, in which each cerata has developed two rings of papillae that match accurately the shape of the hydroid polyps on which it feeds (Rudman 1981a).

Nematocysts are only of defensive value in those aeolids feeding on hydroids, siphonophores, sea anemones and the related zoantharians. In alcyonarians and scleractinian corals, the nematocysts are either too small, or ineffective, and aeolids feeding on these have evolved other defensive strategies (Fig. 16.20C). Many alcyonarian-feeding aeolids take up symbiotic algae from their food and so become camouflaged. As well, most have distasteful and sticky acid glands on the cerata; the cerata are easily autotomised by the aeolid when disturbed. After detachment, the cerata wriggle vigorously for some time. It is assumed that this reaction is startling enough to cause most potential predators to seek elsewhere for food. Coral-eating

aeolids are usually colour camouflaged, either by symbiotic algae from corals such as *Porites*, or by pigments from asymbiotic genera such as *Dendrophyllia*. All species of the genus *Phestilla* have a swollen glandular tip to the cerata (Fig. 16.20D; Pl. 36.1), possibly analogous in some way to use of 'stolen' nematocysts.

Correlation between diversity in colour and shape and environmental factors (especially the species' food) is most strongly developed in those opisthobranchs with the shell reduced or absent. Most of the shelled forms, for example, cephalaspideans, are infaunal burrowers for which camouflage colouration is irrelevant. Among the more specialised cephalaspideans with reduced internal shells, colour can sometimes be assumed to afford camouflage, as in the green herbivorous *Phanerophthalmus*, but in other forms, such as the brightly coloured aglajids, the selective advantage of the colour patterns is obscure (Rudman 1972a, 1973).

The ability of the herbivorous sacoglossans to harbour and cultivate algal plastids in their tissues has been mentioned briefly above. This remarkable symbiosis has been studied by many algal physiologists (Brandley 1984). Different sacoglossans show

various stages in the evolution of such a symbiosis. In some species there seems to be little modification of the gut and the plastids die quickly after ingestion by the slug; there is a high turnover of plastids which may or may not actually be digested and utilised as food. In more advanced species in which the shell is reduced or completely lost, the gut has developed a highly ramified network of ductules through the body wall. Often the body has developed large leaf-like flaps or parapodia (*Elysia*) or aeolid-like cerata down each side (*Stiliger*, *Hermaea*), both of which contain branches of the digestive gland. In many of these species there is clear evidence that plastids are kept alive and photosynthesising to produce carbohydrates and other photosynthetic products used by the sacoglossan.

A parallel to this has been reported recently among nudibranchs (Rudman 1981b, 1981c, 1982a, 1986a, 1987a, 1991b), many species of which feed on cnidarians containing symbiotic dinoflagellates (zooxanthellae) and retain the zooxanthellae alive in their tissues. Some have been shown to obtain significant nourishment from the photosynthetic activities of these stolen organisms (Hoegh-Guldberg & Hinde 1986; Hoegh-Guldberg, Hinde & Muscatine 1986). There is a remarkable parallel with sacoglossans in the evolution of this symbiosis which is best seen in the genus *Phyllodesmium*. Species of *Phyllodesmium* which feed on soft corals lacking zooxanthellae have no unusual modifications to their shape and, like most aeolids, are nearly always found on their food. Some 'primitive' species of *Phyllodesmium* which feed on alcyonarians with zooxanthellae also lack morphological and behavioural modifications. In these species, the zooxanthellae are not retained in the gut for any length of time. At the other extreme are species which are clearly modified for zooxanthellae symbiosis. One of these, *Phyllodesmium longicirrum*, has large paddle-shaped cerata and ducts of the digestive gland ramifying throughout the body wall. In all these ducts large numbers of healthy zooxanthellae are accommodated in special cells. Behaviourally, this species also differs from most aeolids in seldom being found near its food, with the implication that much of its nutritional requirements are met by the symbiotic zooxanthellae. The evolution of zooxanthellae symbioses has occurred independently in nudibranchs at least six or seven times in different aeolid families and among the Dendronotoidea. Although many of the nudibranchs with zooxanthellae symbioses are alcyonarian-feeders, others obtain their zooxanthellae from scleractinian corals, sea anemones, zoantharians and hydroids.

It is evident from the above account that the natural history of most opisthobranchs is tied to their high degree of food specificity, species having evolved strategies that match the life cycles of their prey, be the prey plant or animal. A further illustration can be found in those nudibranchs, some no more than a few millimetres in length, that have apparently been distributed to many parts of the world inadvertently through human activities. Among the polycerid dorids are many examples of species with anomalous distributions clearly tied to shipping activity. In eastern Australia, *Polycera capensis*, originally reported from South Africa in 1824, is now common in the Sydney region; *P. hedgpethi*, originally described from California has been reported recently from South Africa, eastern Australia and New Zealand; and the spectacular *Thecacera pennigera*, which was originally described from England, is now reported from the Mediterranean Sea and the Atlantic, Indian and Pacific Oceans. Other similar examples can be found. A common element is that these nudibranchs all feed specifically on species of bryozoans or other colonial animals which are well-known fouling organisms on the hulls of ships. Prior to such human intervention, the distribution of these nudibranchs was totally dependent on the ability of their larvae to disperse and find food when ready to settle. This is still true, but with the advent of long distance shipping, the prey species has a moveable platform on which to live, thus greatly enhancing the distribution of both the prey and the nudibranch predator. What may never be known is where each of these widespread species originated.

PHYLOGENY

Most opisthobranchs have either very thin shells or none at all, and thus the fossil record is inadequate to document the evolutionary history of the group. Available evidence indicates that opisthobranchs and pulmonates are one very large holophyletic assemblage within the Heterobranchia, a sister group to the Caenogastropoda. Gosliner (1981a) proposed that the 'mesogastropod' Littorinoidea, served as the group of origin for the Heterobranchia. Whatever its origin, the heterobranch stock rapidly underwent an adaptive radiation unparalleled in the Mollusca. This radiation gave rise to eight separate groups of opisthobranchs.

The most primitive living opisthobranchs are contained within the Cephalaspidea (= Bullomorpha). All have a head shield and a Hancock's organ. Some malacologists have advanced the Acteonidae as the most primitive cephalaspidean taxon (for example, Fretter & Graham 1954; Rudman 1972b), whereas Gosliner (1981a) argued for the Ringiculidae. There seem to be unbridgeable gaps between the 'higher' cephalaspidean groups Bulloidea, Philinoidea and Runcinoidea, and Cephalaspidea is almost certainly paraphyletic.

Van der Spoel (1967) derived the Thecosomata (by neoteny) from herbivorous cephalaspideans, nearer the origin of the Pyramidellidae than any other group (note, however, that Pyramidellidae are not grouped with Opisthobranchia in the classification followed here, see Table 15.1). This origin is in approximate agreement with that envisaged by Morton (1979). However, the relationships of the other group of planktonic opisthobranchs, the carnivorous Gymnosomata, are much less evident because its members are greatly modified as active predators. As Morton (1979: 109) stated, 'The gymnosomatous pteropods are a law unto themselves'.

Two holophyletic orders, the Sacoglossa (= Ascoglossa, = Monostichoglossa, = Pellibranchiata) and Anaspidea (= Aplysionomorpha), were also probably derived from herbivorous cephalaspideans. Independently, each followed parallel evolutionary pathways involving shell loss and posterior migration of the mantle complex. Sacoglossans initially specialised on *Caulerpa* (Jensen 1980), a green alga without internal partitions to the thallus and therefore a supplier of great quantities of sap once the thallus wall is punctured. The ancestral sacoglossan was probably very like *Ascobulla* or *Volvatella*, that is, a shallow infaunal bulloid opisthobranch that exploited *Caulerpa* rhizomes (Clark 1982a). The sacoglossan radiation (Clark & Bussaca 1978) went further with this evolutionary trend than did the Anaspidea; indeed, until the 1920s the aeolidiform sacoglossan taxa (families Polybranchiidae and Stiligeridae) were thought to be nudibranchs (Russell 1929).

The Acochlidia is a small and little-known group. Most species are minute and individuals live in water spaces between sand particles, so characters informative of the phylogenetic position of this group may have been lost by simplification. Gosliner (1981a) considered the Acochlidia to be a sister group to the Sacoglossa.

The Notaspidea (= Pleurobranchomorpha) is an example of a group of 'higher' opisthobranchs in which members range from fully shelled to entirely naked. Largely on the basis of the nervous system, Schmekel (1985) advocated that the group is paraphyletic. By contrast Willan (1987a) argued for holophyly, pointing out that because the Umbraculidae exhibit more derived features than the Pleurobranchidae, Schmekel's assumption of the Umbraculidae as ancestral is wrong. *Tylodina* is apparently the most primitive notaspidean: its reproductive system resembles that hypothesised for the ancestral heterobranch; it has an even more primitive configuration than that found today in the supposedly most primitive carnivorous (that is, invertebrate-grazing) cephalaspideans. Notaspideans developed specialised body forms, their diets radiating from the ancestral sponge feeding (Willan 1984a).



PLATE 22: GASTROPODA

- 1,2 *Cellana tramoserica* (Nacellidae), a dominant intertidal limpet of southern and eastern rocky shores, grazes microalgae close to its home site.
- 3 The exhalant current, with waste products, is expelled through the shell apex in keyhole limpets, such as *Amblychilepas nigrita* (Fissurellidae).
- 4 Respiratory holes, as seen in *Haliotis asinina*, are typical of all haliotids. They direct the flow of the exhalant, and some of the inhalant, currents.
- 5 Large populations of *Haliotis laevigata* (Haliotidae) occur on the southern Australian coast, where this and other *Haliotis* species are fished commercially.

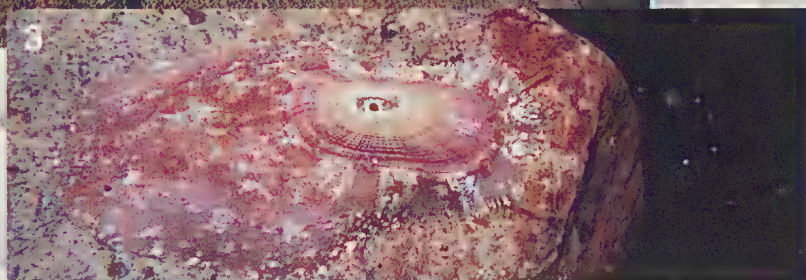


PLATE 23: GASTROPODA

- 1 The periwinkle *Nodilittorina pyramidalis* (Littorinidae) survives exposure to air in and above the splash zone of rocky shores.
- 2 *Littoraria cingulata* (Littorinidae) lives on the trunks, leaves and, occasionally, roots of mangrove trees of north-western Western Australia.
- 3 The common intertidal grazer *Nerita atramentosa* is the only southern Australian representative of the typically tropical Neritidae.
- 4 The bright colours seen here in the top shell *Calliostoma armillatum* are common among trochids; shells may also be strongly patterned.
- 5 *Clanculus undatus* (Trochidae) shelters under rocks on reefs along the southern coast, and emerges at night to feed on algal film.
- 6 The intertidal grazers *Austrocochlea constricta* (Trochidae) are extremely common on southern and south-eastern rocky shores; the width of the distinct shell bands varies individually.



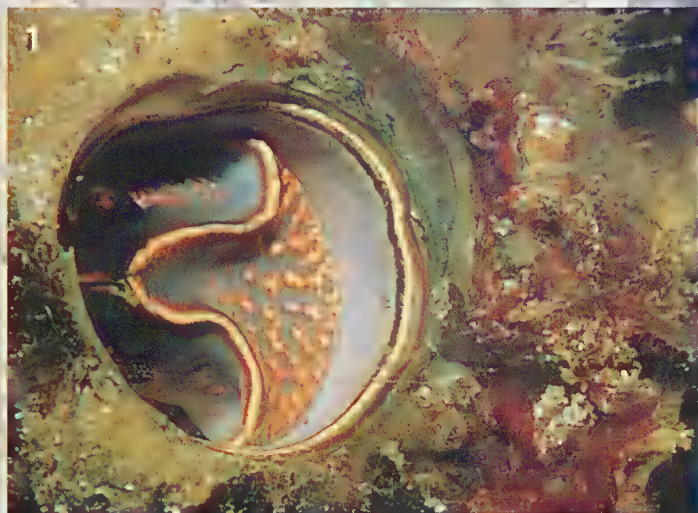


PLATE 24: GASTROPODA

- 1 The sessile vermetid *Serpularia siphon* secretes mucous threads to catch food particles and plankton.
- 2 Mud whelks *Terebralia palustris* (Potamididae) live on the mud surface in northern Australian mangroves.
- 3 An *Ataxocerithium* species – just one of the species of the little known Australian cerithioid fauna.
- 4 The bubble shell, *Janthina janthina* (Janthinidae), preys on bluebottles and other neustonic cnidarians.
- 5 Eulimids are primarily ectoparasitic on echinoderms; these *Eulima* species are attached to the oral surface of a red crinoid.
- 6 The strong axial varices seen in *Epitonium* species (Epitoniidae) are typical of most wentletraps. They feed largely on corals.

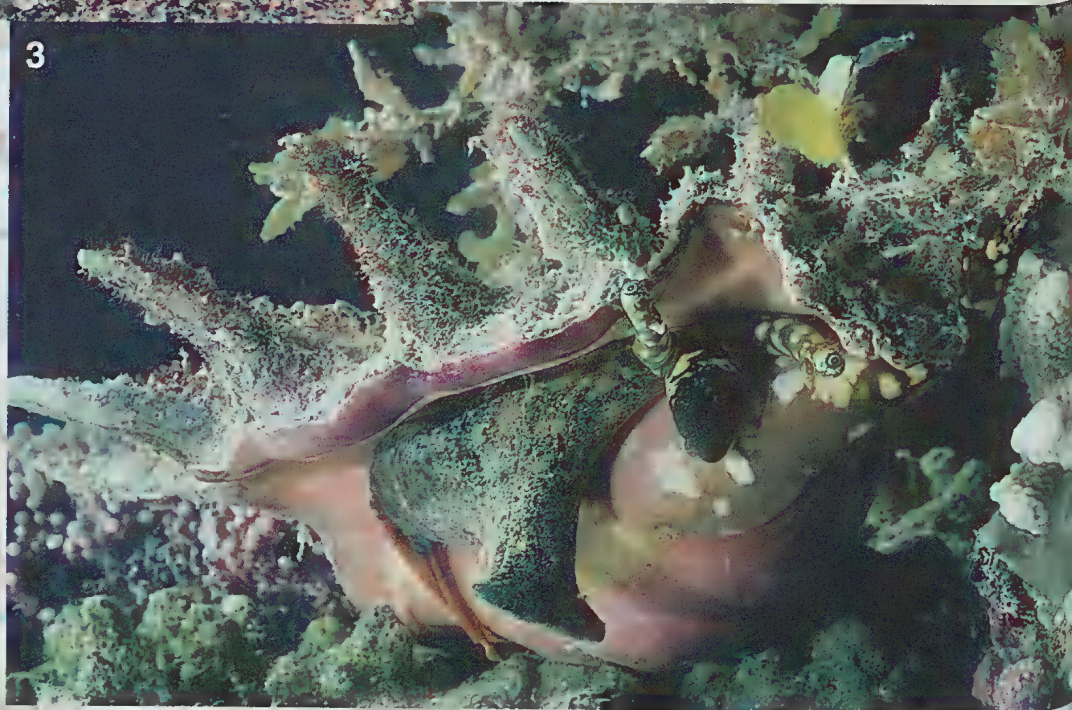


PLATE 25: GASTROPODA

- 1 The stromb *Strombus luhuanus* (Strombidae) burrows in the sand to lay its eggs; each elongate gelatinous egg mass may contain 500 000 eggs.
- 2 The U-shaped notch of *Strombus aurisdianae* (Strombidae), typical of most adult strombs, forms a peephole for the right eye; the right eye stalk is shorter than the left, which extends in front of the shell.
- 3 The operculum of *Lambis lambis* (Strombidae) is too small to close the shell opening; the animal uses it to push on the substratum, for righting itself if necessary or for defence.
- 4,5 *Capulus australis* (Capulidae) usually attaches permanently to scallop shells; egg capsules, brooded underfoot, are visible in the inverted adult.



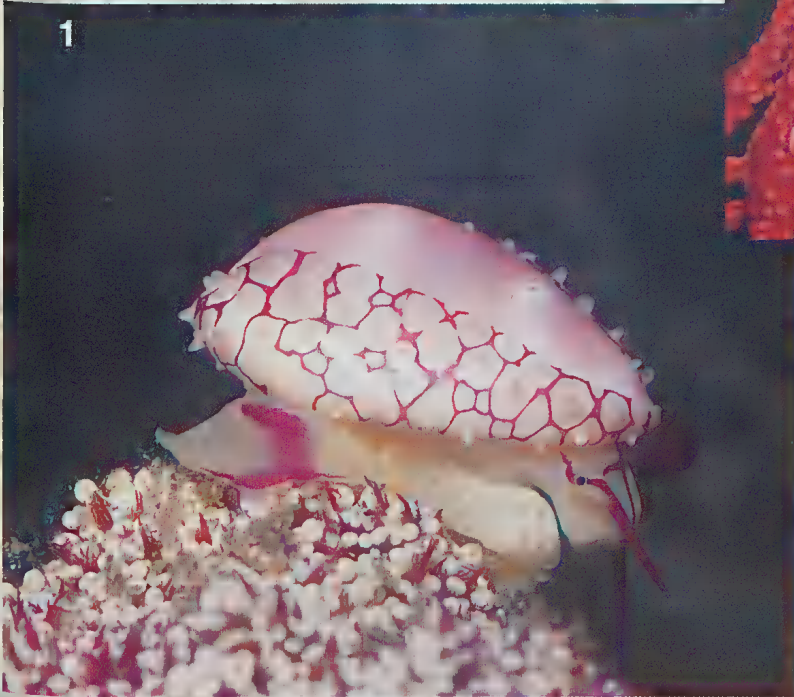


PLATE 26: GASTROPODA

- 1 The egg cowry *Prionovolva brevis* (Ovulidae) usually lives and feeds on a specific cnidarian. It occurs to depths of 10 m along the east coast.
- 2 The shell and mantle colours of many spindle cowries (Ovulidae) mimic those of their specific host coral for camouflage.
- 3 The lamellariid *Lamellaria australis* feeds on ascidians. It lives under rocks along the southern and eastern coasts.
- 4 *Ellatrivia merces* (Triviidae) is a very common inhabitant of the intertidal zone down to 15 m depth; it is often found on bryozoan colonies.
- 5 The tropical eyed-cowry, *Cypraea argus*, shows the colourful mantle and patterned shell typical of most cypraeids.
- 6 The small cypraeids of the *Notocypraea* group, including *Cypraea comptoni*, are variable and difficult to identify. Eggs of all species develop directly into crawling young.

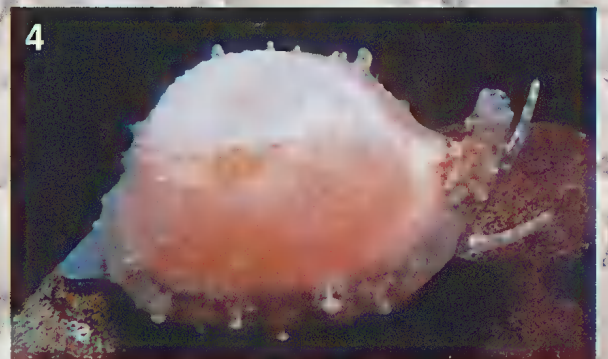
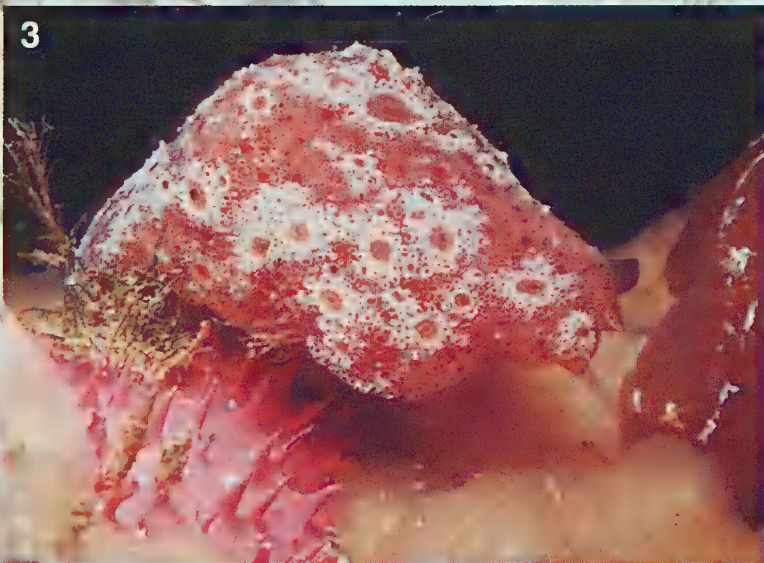
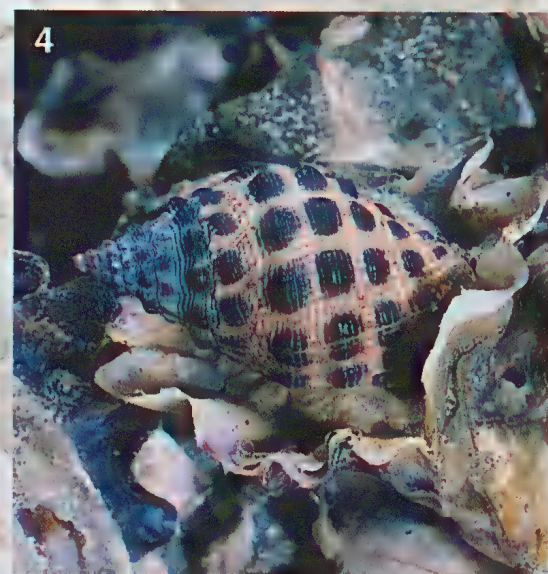




PLATE 27: GASTROPODA

- 1 *Naticarius alapapilionis* (Naticidae) ploughs through the sand in search of molluscan prey. It extracts the flesh of its prey through a hole drilled in the shell.
- 2 The epipelagic heteropod *Atlanta gaudichaudi* (Atlantidae) is an active carnivore, as evident from the fish in its gut.
- 3 Typical of all cassids, *Semicassis adcocki* burrows in the sand. Cassids feed largely on sea urchins and their kin.
- 4 Muricids such as *Murex acanthostephes* attack and drill holes in the shells of other molluscs, using the joint action of the radula and acid secretions.
- 5 The common mulberry shell, *Morula marginalba* (Muricidae), is a major pest species in commercial oyster farms in eastern Australia.
- 6 The whelk *Nassarius particeps* (Nassariidae) is an active scavenger on intertidal mud and sand flats and rocky shores of southern and eastern Australia.



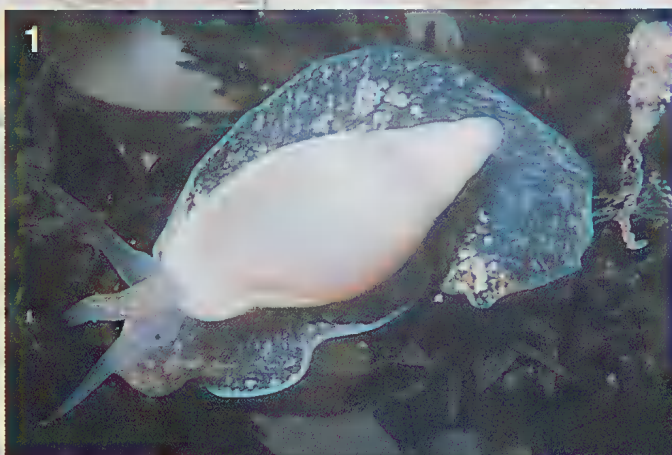


PLATE 28: GASTROPODA

- 1 *Cystiscus multidentatus* (Marginellidae), a predator on sessile invertebrates, occurs widely on reefs of the southern Australian continental shelf.
- 2 *Austroginella tasmanica* (Marginellidae), a predator on benthic invertebrates, is common in shallow sandy habitats of south-eastern Australia.
- 3 The brilliant blue periostracum of the sapphire spindle shell *Latirus spiceri* (Fascioliariidae) is easily removed after death.
- 4 Like most other volutids, *Amoria exoptanda* is a nocturnal predator on molluscs and other small animals. It occurs from South Australia to southern Western Australia.
- 5 One of the largest volutes, *Melo amphora* may grow to 560 mm. The common name 'baler shell' arises from their use by Aborigines to bail water from their canoes.





PLATE 29: GASTROPODA

- 1 Architectoniscids emerge at night to feed on colonial cnidarians; they live down to depths of 150 m.
- 2 The large muscular foot may expand over the shell of *Ancillista muscae* (Olividae). Using its foot, the animal ploughs just below the sand surface.
- 3 *Cancellaria spirata* (Cancellariidae) lives in sand pockets on reefs on medium energy coasts, feeding at night on small gastropods.
- 4 *Conus striatus* (Conidae) lays flat pouch-like egg capsules, each containing many eggs. This is one of the few cone species that kill and eat fish.
- 5 The typical conid proboscis or rhynchodeum, seen here beneath the protruded siphon of *Conus anemone* (Conidae), is used to direct venom-bearing radular teeth towards selected prey.



PLATE 30: GASTROPODA

- 1 *Crenavolva tigris* (Ovulidae) is widely distributed in the tropical Indo-Pacific. It feeds on species of the gorgonian genus *Euplexaura*, as seen here.
- 2 Adults of the nearly-transparent pelagic nudibranch *Phylliroe* species (Phylliroidae) feed on medusae (*Zanclea*), larvaceans (*Oikopleura*) and other plankters near the surface at night, where they luminesce brilliantly.

2





PLATE 31: GASTROPODA

- 1 *Atopos australis* (Rathouisiidae), a carnivorous slug of eastern tropical and subtropical forests.
- 2 *Bothriembryon barretti* (Bulimulidae) shelters and aestivates among rocks on the arid Nullabor Plain.
- 3 The light shell and enlarged head region enable the rhytidid *Victaphanta compacta* to manage large prey.
- 4 *Cassidula rugata* (Ellobiidae) browses sediments of tropical estuaries.
- 5 The strong resemblance to the intertidal pulmonate *Siphonaria diemenensis* (Siphonariidae) to limpets is characteristic of this group.





PLATE 32: GASTROPODA

- 1 The arboreal camaenid *Rhynchotrochus macgillivrayi* occurs in wet forests of northern Queensland.
- 2 *Hadra bipartita*, a terrestrial camaenid of tropical rainforests in Queensland.
- 3 An undescribed 'semi-slug', *Helicarion* species (Helicarionidae), known only from Mt Tamborine, Queensland.
- 4 The shell of the litter browser *Pandofella whitei* (Caryodidae) is reduced.
- 5 Golden morph of *Triboniophorus graeffei* (Athoracophoridae) from Mt Superbus, Queensland.



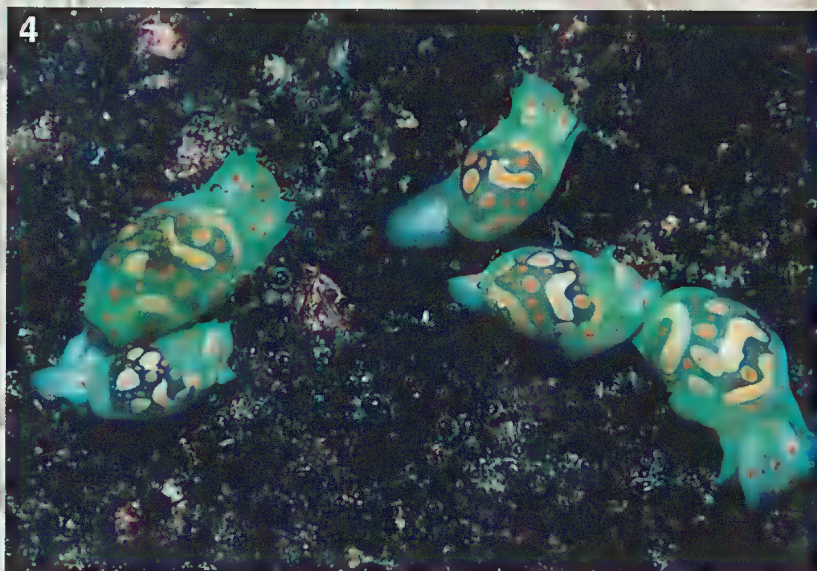
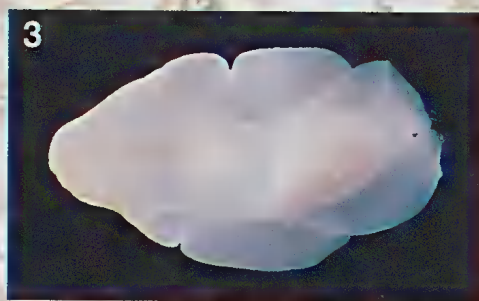
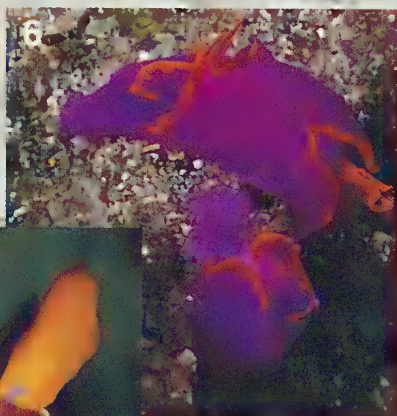


PLATE 33: GASTROPODA

- 1 *Bullina lineata* (Bullinidae) is typical of the many 'sea-slugs' which still retain a large external shell.
- 2 The shell of the tailed slug *Chelidonura inornata* (Aglajidae) is reduced to a small internal plate.
- 3 *Philine angasi* (Philineidae) crushes the shells of its bivalve food with calcareous gizzard plates.
- 4 *Haminoea simillina* (Haminoeidae) grazes on filamentous algae in shallow tropical to temperate seas.
- 5,6 Bat-wing slugs, *Sagaminopteron ornatum* (Gastropoda), use their parapodia for swimming. They are often found on sponges, *Dysidea* species, but their food, and that of all gastropods, remains unknown.
- 7 The side-gilled slug, *Pleurobranchus peronii* (Pleurobranchidae), widespread in the tropical Indo-West Pacific, preys on ascidians.



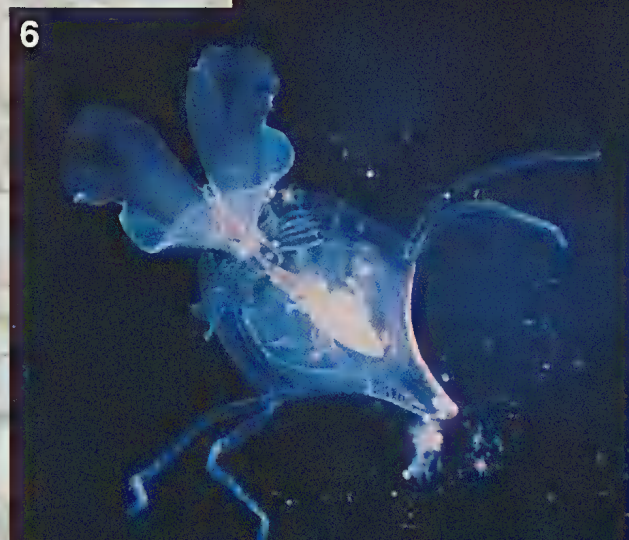
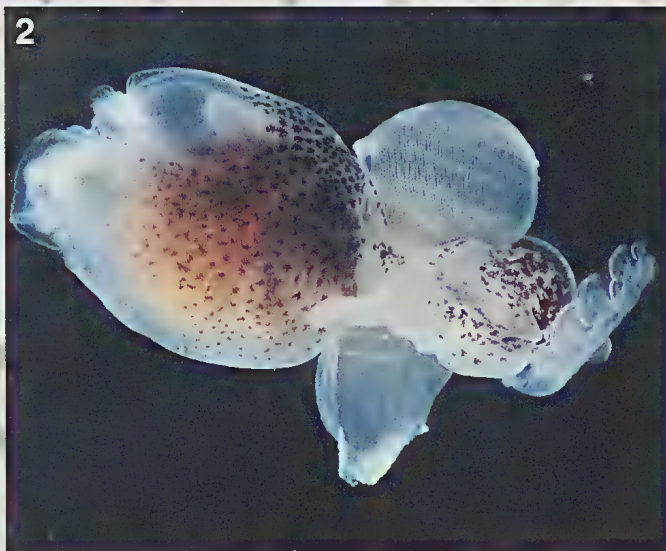


PLATE 34: GASTROPODA

- 1 Only following observations of living specimens was it clear that the sacoglossan *Tamanovalva babai* (Berthellinidae) is a remarkable bivalved gastropod.
- 2 The suckered arms of the gymnosome pteropod *Pneumodermopsis heronensis* (Pneumodermatidae) are reminiscent of those of cephalopods.
- 3 Sacoglossans are the 'bugs' of the sea, sucking the cell contents from their food algae. *Oxynoe* species (Oxynoidae) live and feed on *Caulerpa* species.
- 4 *Aplysia sydneyensis* (Aplysiidae). The common name of the herbivorous sea hares arose in classical Greece from their resemblance to the European hare.
- 5 *Creseis chierchiae*. Cavoliniids escape by flapping the wings which protrude from the shell aperture.
- 6 The appendages and bilobed velum of a cavoliniid veliger form flotation devices typical of many plankters.

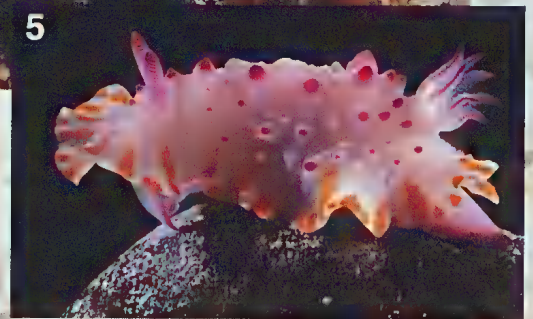
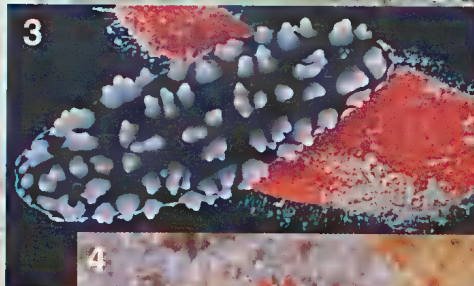
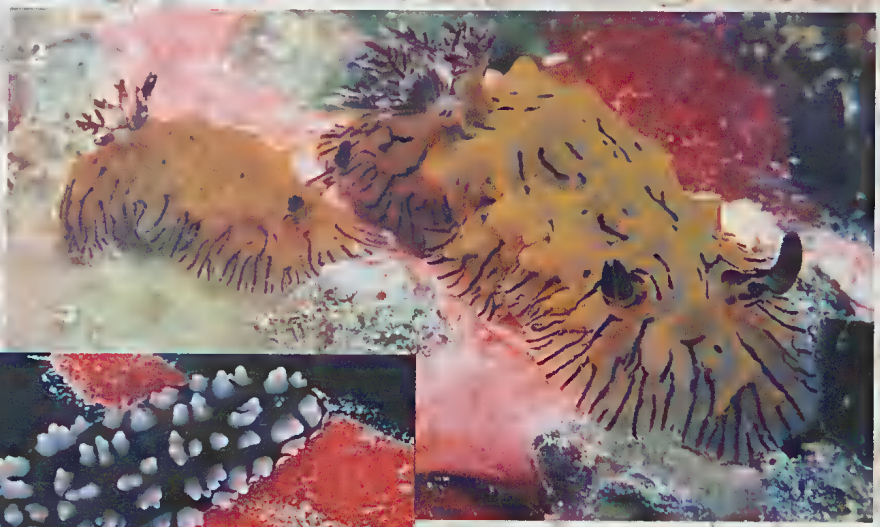
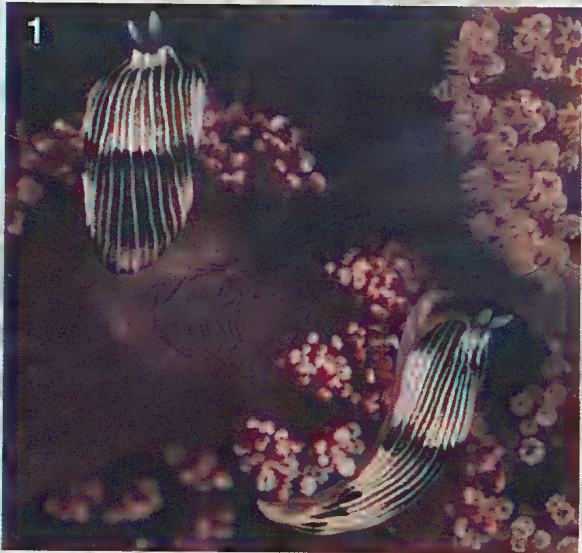
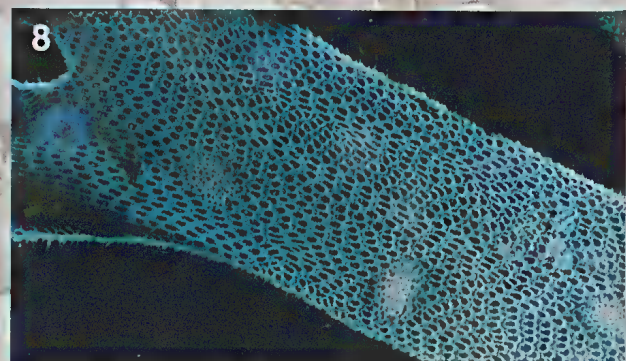
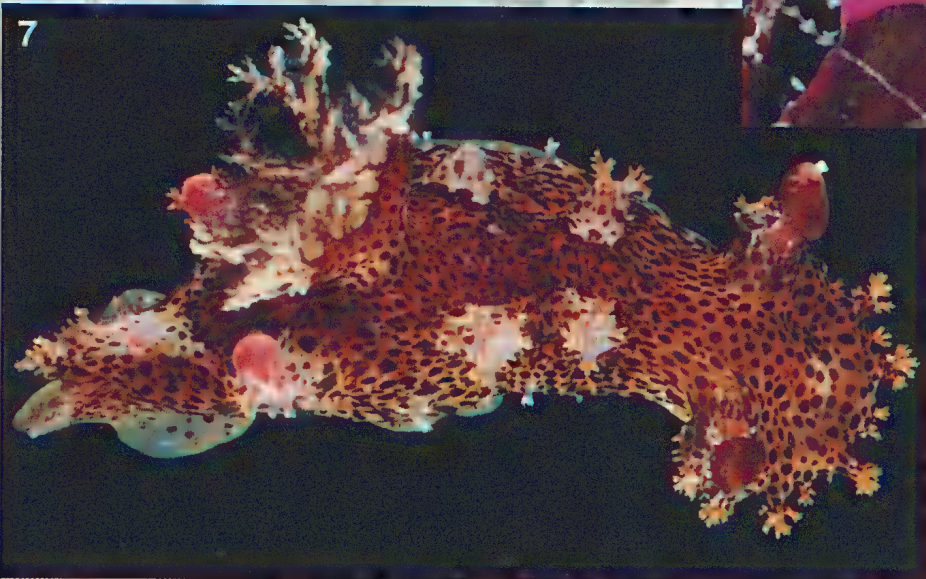


PLATE 35: GASTROPODA

- 1 Like other species of *Dermatobranchus* (Arminidae), this unnamed form is associated with particular species of alcyonarian soft coral.
- 2 *Halgerda willeyi* (Dorididae) is widely distributed from the Great Barrier Reef to East Africa and the Red Sea.
- 3 Secretions of toxic chemicals from the mantle glands of *Phyllidiella pustulosa* (Phyllidiidae) are thought to deter predation by fishes.
- 4 *Chromodoris kuiteri* (Chromodorididae), is one of many brilliantly coloured members of this family in Australian waters.
- 5 Like most chromodoridids, *Mexichromis macropus* is usually associated with the specific sponge on which it feeds.
- 6 Species of *Hopkinsia* (Goniodorididae) associate with, and mimic the colour and form of bryozoans, genus *Pleurotoichus*.
- 7 When disturbed *Plocamopherus imperialis* (Polyceridae) produces luminescent flashes from its 'light organs' and other parts of its body.
- 8 This *Doridella* species (Corambidae) is one of several worldwide that feed on encrusting bryozoans, *Membranipora*, its lace-like colour pattern matching that of its host.



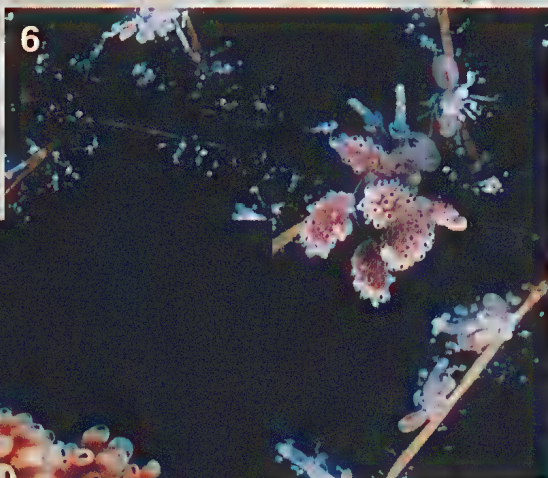
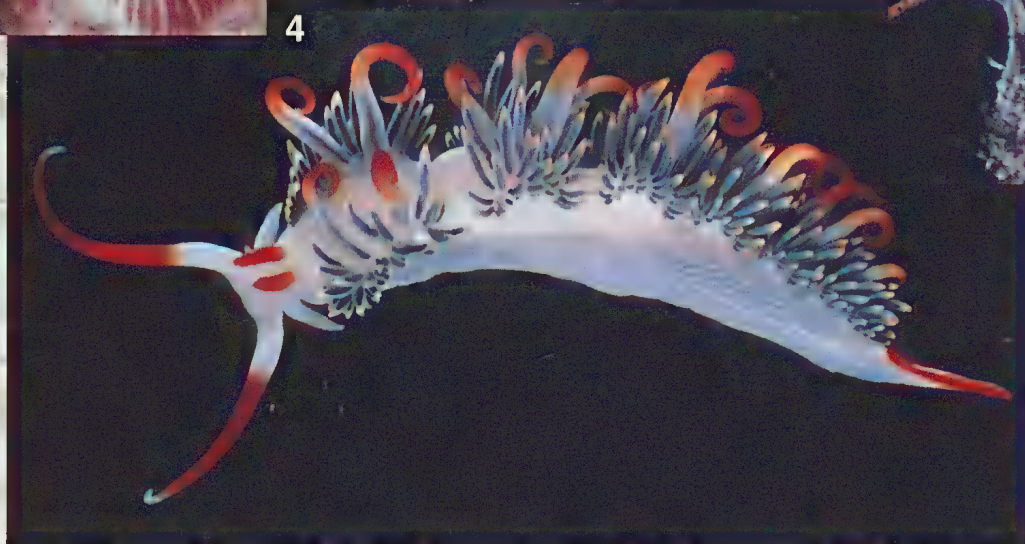
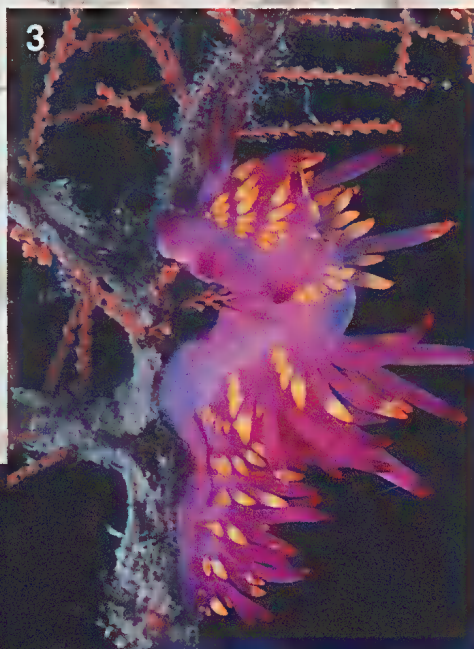


PLATE 36: GASTROPODA

- 1 *Phestilla melanobranchia* (Tergipedidae) feeds on, and matches in colour, one of several related species of dendrophyllid corals.
- 2 Like many small aeolids, *Eubranchius inabai* (Eubranchidae) associates with epiphytic hydroids growing on brown algae.
- 3 *Cuthona sibogae* (Tergipedidae), a hydroid predator, lives on shallow reefs, often in large numbers.
- 4 *Phidiana brocki* (Glaucidae) stores nematocysts from its cnidarian prey in the red tips of its cerata. When disturbed, the cerata stand erected, apparently as a warning display.
- 5 The large oral hood of *Melibe* species (Tethydidae) is used to capture small crustaceans.
- 6,7 Common in intertidal rock pools of south-eastern Australia, *Doto ostenta* (Dotidae) feeds on hydroids.
- 8 Like most tritoniids, this species of *Marionia* resembles its soft coral host in shape and colour.

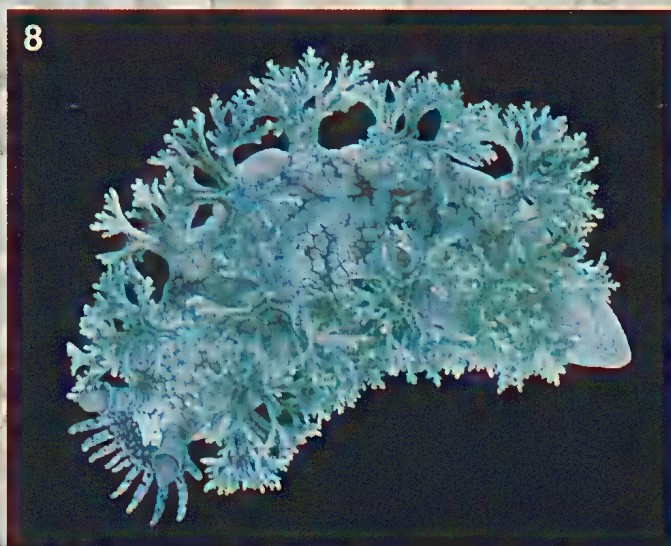
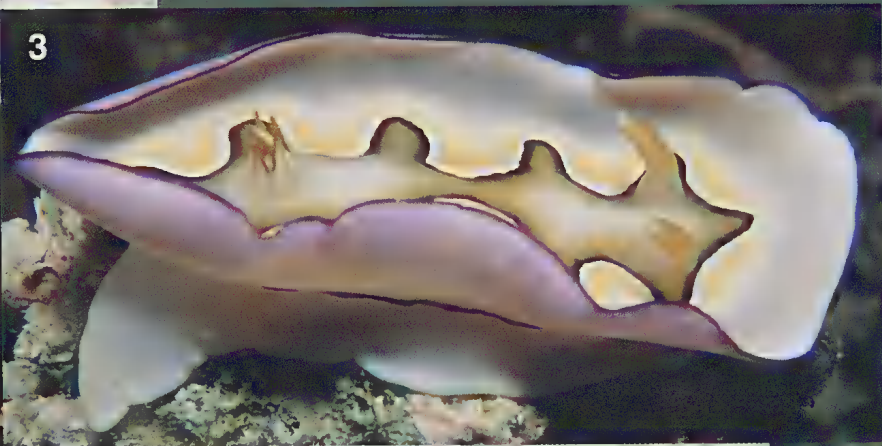
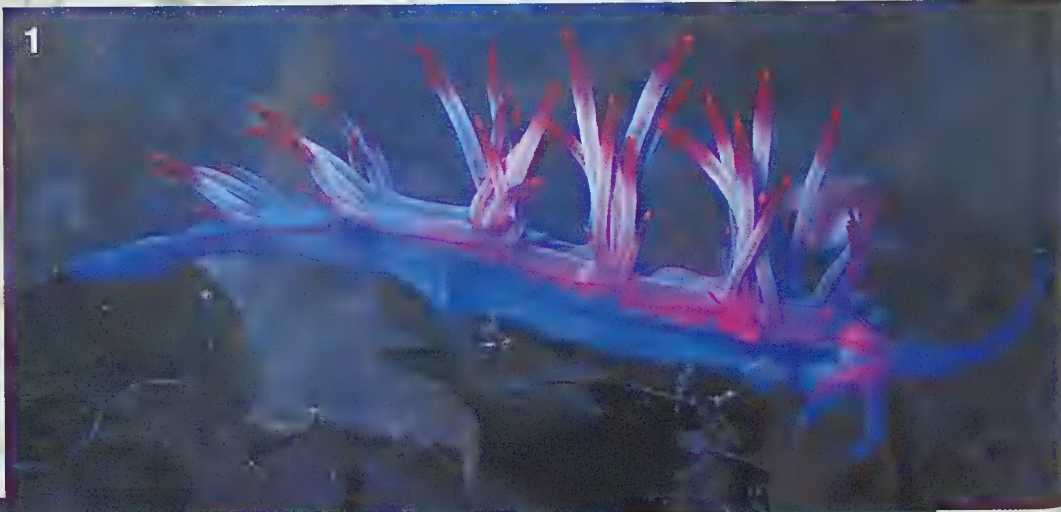


PLATE 37: GASTROPODA

- 1 *Flabellina rubrolineata* (Flabellinidae) stores nematocysts from hydroid prey in cnidosacs on the tips of the cerata.
- 2 *Roburnella wilsoni* (Oxynoidae) feeds on species of the algal genus *Caulerpa*.
- 3 The mantle of *Chromodoris coi* (Chromodorididae), a common West Pacific species, undulates rhythmically during crawling.
- 4 *Nembrotha* cf. *lineolata* (Polyceridae), part of a wide-spread species complex, feeds on ascidians on shallow reefs.



The Nudibranchia is probably both monophyletic (although this is contested) and a sister group to the Notaspidea. Certainly none of its members are at all derivable from extant side-gilled sea slugs and it is more plausible to derive nudibranchs, either monophyletically or diphyletically, from long-extinct carnivorous invertebrate-grazing cephalaspidean-like ancestors. Two very different nudibranch clades came to dominate the entire Opisthobranchia in terms of adaptive diversity and numbers of species – the Anthobranchia (= Eucteniidae; = Cteniidae) and the Cladobranchia (= Acteniidae). Members of the former group are generally larger, have mid-dorsal, circumanal gills and are (primitively) sponge rasps. Members of the latter group are generally smaller, have lateral respiratory structures, and (primitively) a lateral anus, and prey on cnidarians. Parallelism is 'rampant' (Gosliner & Ghiselin 1984), both between these groups and especially between the separate lineages within the Cladobranchia. That the radiation of the nudibranchs was driven, at least in part, by visually acute predators like fishes is inferred from the numerous morphological and chemical defences exhibited by nudibranchs.

BIOGEOGRAPHY

The Opisthobranchia is basically a tropical group of molluscs; its numbers attenuate rapidly in temperate waters. About 1000 opisthobranch species occur in northern Australia, but further south in central New South Wales this number has more than halved. Northern Tasmania, Victoria and South Australia have about 400 species (Burn 1989). Fewer species (about 150) occur in southern Tasmania (Willan & Coleman 1984). Only about 50 species are known from those Subantarctic and Antarctic waters adjacent to Australian territories. This numerical gradient reflects both a quantitative and a qualitative impoverishment in the opisthobranch fauna. Several large families – Aglajidae, Elysiidae, Polybranchidae, Gymnodorididae, Polyceridae, Aegiretidae (= Notodorididae), Chromodorididae, Phyllidiidae, Arminidae – are essentially only tropical with few or no representatives in cool-temperate waters. No additional large families achieve dominance in lower latitudes.

Australia has two distinct opisthobranch faunas – a tropical northern one and a cool-temperate southern one. These faunas have wide zones of overlap along the continent's east and west coasts. The majority of tropical benthic species occur naturally throughout the vast Indo-West Pacific Ocean (for example, *Plakobranthus ocellatus*, *Pleurobranchus peronii* (Pl. 33.7), *Glossodoris atromarginata*, *Phyllidia varicosa*, *Bornella anguilla*). Some extend into the Caribbean Sea (for example, *Stylocheilus longicauda*, *Hexabranthus sanguineus*, *Lomanotus vermiformis*) and a few occur in warm temperate and tropical seas all round the world (for example, *Aplysia juliana*, *A. parvula*, *Umbraculum umbraculum*, *Berthella stellata*). Rudman (1987b) has cautioned, however, that some species presently interpreted as being widespread in the Indo-West Pacific could actually be complexes of species each with a more restricted range. If this is so, it is likely that some tropical species will be found to be confined to Australia's sector of the western Pacific when adequate collecting data are analysed (presently such analysis is impossible). At present, not one species of opisthobranch can be reliably identified as a probable northern Australian endemic, at least not one confined to the Great Barrier Reef or coral reefs off northern Western Australia. However, *Armina cygnea* is one nudibranch with, apparently, an exclusive circum-Australian distribution.

Endemic taxa characterise the faunas of the overlap and southern Australian biogeographic realms. Presently, nine genera (*Aporodoris*, *Australiaeolis*, *Austrocylichna*, *Digidentis*, *Ilbia*, *Nossis*, *Paliolla*, *Roburnella* (Pl. 37.2) and *Verconia*) have been found only in southern Australia, and a further three (*Austrodoris*, *Caldukia*, *Tularia*) are confined to Australia and New Zealand. *Caldukia* has one species in Australia (*C. affinis*) and two others in New Zealand (*C. rubiginosa* and *C. albolineata*). Endemism is high at the species level, even in widespread genera. Virtually all

the endemic species can be derived from tropical ancestors (for example, some *Edentellina* species, *Polybranchia pallens*, *Pleurobranchus hilli*, and *Ceratosoma brevicaudatum*). Some 20 eastern Australian opisthobranchs, 11 of them nudibranchs (Willan 1989), also occur in New Zealand (among them, *Archidoris wellingtonensis*, *Berthella medietas*, *Dermatobranchus pulcherrimus*, *Philinopsis taronga*, *Trapania brunnea*). About a dozen species of hardy tropical opisthobranchs live, and can apparently reproduce, in South Australia (Burn 1977; Plant 1977).

Presently, six benthic nudibranch species are recognised that almost certainly have become established in Australia since the arrival of Europeans. These vagrant species, introduced accidentally by shipping, are *Polycera capensis*, *P. hedgpethi*, *Thecacera pennigera*, *Okenia plana*, *Janolus hyalinus* and *Godiva quadricolor*.

Most planktonic opisthobranchs occur in all tropical and temperate seas (warm as well as cool), demonstrating that the factors controlling their distribution differ from those affecting benthic taxa. Examples of such 'cosmopolitan' opisthobranchs are *Limacina inflata*, *Creseis acicula*, *Cavolinia gibbosa* and *Pneumodermopsis paucidens*.

METHODS OF STUDY

The study of opisthobranchs is not as straightforward as that of shelled molluscs. Ideally opisthobranchs should be examined alive soon after collection because all known methods of preservation result in colour loss, shrinkage and bodily deformation, especially in the shell-less groups. The living specimen should be sketched or photographed and details of its body form, colouration and behaviour recorded. For identification it is desirable to have both a colour photograph of the live animal and an adequately preserved specimen.

Recording the length of opisthobranchs presents special difficulties because of their deformable bodies and such difficulties have necessitated the adoption of standard conventions. All measurements should be made while the animal is active. Maximum shell length is recorded for shelled specimens and maximum extended crawling length of the actual body is recorded for shell-less species and for those with internal shells. This measurement is taken from the anterior margin of the head or oral veil (not the tips of the oral tentacles) to the end of the foot when the specimen is crawling in a straight line. In dorid nudibranchs, the head and foot are usually hidden beneath the mantle even when the specimen is crawling, so the convention used by students of this group is to measure maximum mantle length only (even if the posterior section of the foot is visible behind the mantle, its length is not added to that of the mantle). Usually several measurements are taken and the greatest value is recorded because this represents the maximum length the specimen can attain. If length is recorded following this standard method, comparable data sets can be obtained for use in growth and ecological studies.

If the specimen is not required for research purposes, it should be returned to the sea after it has been studied. Few opisthobranch species can be kept for their full life span in aquaria because their food species (particularly sponges, hydroids, ascidians and bryozoans) die rapidly in captivity. Unlike their shelled caenogastropod kin, the shell-less opisthobranchs make poor subjects for collections, being for the most part neither attractive when preserved nor easily displayed.

If the specimen is to be preserved it should first be relaxed to retain, to the extent possible, its original body shape. The process of relaxation or narcotisation uses drugs to block the specimen's response to stimuli. The simplest narcotising chemicals are magnesium sulphate or magnesium chloride (8% solution in each case) or menthol crystals. The chemical should be added little by little to the seawater containing the specimen rather than being administered as a large single dose. Other suitable but less commonly used mild narcotising chemicals are propylene phenoxetol, chloral hydrate and chloretone. It often helps to chill the specimen in a refrigerator during the narcotisation process.

16. OPISTHOBRANCHIA

When the specimen is fully narcotised, it should be completely extended and no part of its body should contract when touched by a needle. Small or delicate specimens take about two hours to narcotise, but others like aglajids and intertidal dorids, can take 24 hours or longer. It is important to fix and preserve the specimen as soon as it is narcotised because tissue disintegration commences immediately after death.

All opisthobranchs should be stored permanently in preservative fluid, that is in the 'wet' state. Shell-less opisthobranchs can be stored in 10% neutral formalin, 70% ethyl alcohol or 70% isopropyl alcohol. Formalin is preferable because it fixes the specimen in a better condition for dissection. Bouin's fluid is recommended if tissues are to be examined histologically. If possible, the shell should be removed from shelled opisthobranchs after narcotisation, or the whole specimen preserved in alcohol.

Descriptions of opisthobranchs place a heavier reliance on body form, the digestive system, the nervous system and the reproductive system, than on the shell. Of course, in those taxa where there is no shell, the description can only be based on body form and internal organ systems. Caution needs to be exercised because all of these characters alter to some degree with maturity of the specimen (ontogenetic variation) and preservation (artefacts), so several specimens should be dissected and the description should be as comprehensive as possible. Many of the

earlier descriptions of opisthobranchs cannot be matched to living specimens because they are typological (that is, they relate solely to the specimen under observation; see History of Discovery).

Opisthobranch taxonomy places great reliance on the form of the radula and jaws. After examination of the complete alimentary system, the pharyngeal bulb should be excised and placed in caustic fluid in order to dissolve the musculature off the cuticularised structures within. A hot solution of 10% potassium hydroxide is routinely employed for this purpose. A 50% hypochlorite solution is recommended for treatment of tiny specimens; although this solution takes longer to dissolve the musculature, there is less chance of losing the radula or jaws. After extraction, these structures should be washed in distilled water and mounted for examination. Traditionally, descriptions of the radula and jaws were made on the basis of stained preparations on microscope slides, but nowadays many are based on scanning electron microscope preparations.

CLASSIFICATION

The rank accorded to the Opisthobranchia by authors varies; see discussion in Chapter 15 and Table 15.1. The status accorded to component taxa would thus also be varied. The arrangement followed in this Chapter is outlined in Table 16.1.

Table 16.1 Summary of opisthobranch families. Arrangement of Cephalaspidea is modified after Odhner (1939). Families not found in Australian waters are indicated with an asterisk. According to the arrangement of Ponder & Lindberg (1996), the Opisthobranchia would be at ordinal level if ranked, and thus ordinal and subordinal taxa in this table would be relegated to a lower level (see also position of Opisthobranchia in Table 15.1).

OPISTHOBRANCHIA

Order CEPHALASPIDEA

Superfamily ACTEONOIDEA

- Family Acteonidae
- Family Bullinidae
- Family Hydatinidae

Superfamily RINGICULOIDEA

- Family Ringiculidae

Superfamily CYLINDROBULLOIDEA

- Family Cylindrobullidae*

Superfamily DIAPHANOIDEA

- Family Diaphanidae

Superfamily PHILINOIDEA

- Family Cylichnidae
- Family Retusidae
- Family Philinidae
- Family Philinoglossidae*
- Family Aglajidae
- Family Gastropteridae

Superfamily HAMINOEOIDEA

- Family Haminoecidae
- Family Bullactidae*
- Family Smaragdinnellidae
- Family *Incertae sedis*

Superfamily BULLOIDEA

- Family Bullidae

Superfamily RUNCINOIDEA

- Family Runcinidae
- Family Ilbiidae

Superfamily INCERTAE SEDIS

- Family Notodiaphanidae*

Order ACOCHLIDEA

Superfamily ACOCHLIDIOIDEA

- Family Acochlididae*
- Family Hedylopsidae*

Superfamily MICROHEDYLOIDEA

- Family Asperspinidae*
- Family Microhedyllidae
- Family Ganatidae

Order RHODOPEMORPHA

- Family Rhodopidae

Order SACOGLOSSA

Superfamily OXYNOOIDEA

- Family Volvatellidae
- Family Oxynoidae
- Family Juliidae

Superfamily ELYSIOIDEA

- Family Plakobranchidae
- Family Elysiidae
- Family Boselliidae*
- Family Gascoignellidae*
- Family Platyhedyllidae*

Superfamily LIMAPONTIOIDEA

- Family Caliphyllidae
- Family Costasiellidae
- Family Hermaeidae
- Family Limapontiidae

Order ANASPIDEA

Superfamily AKEROIDEA

- Family Akeridae

Superfamily APLYSIOIDEA

- Family Aplysiidae

Order NOTASPIDEA

Superfamily TYLODINOIDEA

- Family Tylodinidae
- Family Umbraculidae

Superfamily PLEUROBRANCHOIDEA

- Family Pleurobranchidae

Order THECOSOMATA

- Family Limacinidae
- Family Cavoliniidae
- Family Peraclidiidae
- Family Cymbuliidae
- Family Desmopteridae

Order GYMNOSOMATA

Suborder GYMNOSOMATA

- Family Pneumodermatidae
- Family Notobranchaeidae
- Family Cliopsidae
- Family Clionidae

Suborder GYMNOPTERA

- Family Hydromyidae

Order NUDIBRANCHIA

Suborder DORIDINA

Superfamily ANADORIDOIDEA

- Family Corambidae
- Family Goniodorididae
- Family Onchidorididae
- Family Polyceridae
- Family Gymnodorididae
- Family Aegiretidae
- Family Vayssielaide

Superfamily EUDORIDOIDEA

- Family Hexabranchidae
- Family Dorididae
- Family Chromodorididae
- Family Dendrodorididae
- Family Phyllidiidae

Suborder DENDRONOTINA

- Family Tritoniidae
- Family Bornellidae
- Family Marianinidae
- Family Hancockiidae
- Family Dotidae
- Family Scyllaeidae
- Family Tethydidae
- Family Phylliroidae
- Family Lomanotidae

Suborder ARMININA

- Family Arminidae
- Family Doridomorphidae
- Family Charcotiidae
- Family Madrellidae
- Family Zephyrinidae
- Family Pinufiidae

Suborder AEOLIDINA

- Family Flabellinidae
- Family Eubranchidae
- Family Acolidiidae
- Family Glaucidae
- Family Embletoniidae
- Family Tergipedidae
- Family Fionidae

Order CEPHALASPIDEA

This group contains descendants of the original burrowing opisthobranch stocks that have persisted relatively unchanged to the present day, such as *Acteon*, *Pupa* and *Ringicula*. Some cephalaspideans have evolved in the direction of more complete adaptation to the burrowing life, and these forms (*Philine* is a good example) ingest infaunal bivalve molluscs and crush them in the stomach. This way of life was accompanied by shell-reduction and eventual loss of the shell, as well as the rearward displacement of the organs of the mantle cavity, and the loss of the ancestral streptoneury. Another distinctive line of evolution within the Cephalaspidea involved the adoption of herbivory (for example, the superfamilies Bulloidea, Haminoeioidea and Runcinoidea). Nevertheless, the Cephalaspidea are largely a carnivorous group, dominating the shallow marine sandy and muddy environments which offer a rich harvest of relatively immobile bivalves, polychaetes and foraminiferans.

The shell may be external, internal, or absent in the adult. An operculum is present in the adult only in the Acteonidae, in some Cylichnidae and Retusidae and in *Bullina lineata* (Bullinidae) (R.C. Willan personal communication). The head often forms a flattened burrowing cephalic shield, sometimes with tentacular processes at the front and rear. Paired chemoreceptors, the Hancock's organs, occur below the antero-lateral edges of the cephalic shield. The mantle cavity may be antero-lateral, capacious and more or less enclosed, or may be more open and occupy a posterior position (in the most advanced forms). A plicate gill is usually present. The mantle is often reduced in size, but is sometimes substantial, forming part of the dorsal integument and sometimes produced to form an external posterior pallial lobe. The foot often bears expanded parapodial lobes, which may function as swimming organs. Mandibles are uncommon but a radula is usually present; obsolete teeth are discarded, not retained in a special sac. A grinding gizzard is often present, containing a number of calcareous or horny plates. The hermaphroditic reproductive system usually (but not always) displays an open, external, ciliated autospermal groove, which leads to the penis on the right side of the body; fertilisation is vaginal or by spermatophore, never hypodermic. The central nervous system is usually euthyneurous, but not greatly concentrated. The cerebral collar encircles the foregut, generally anterior to the buccal bulb.

Worldwide, the Cephalaspidea contains eight superfamilies and about 20 families, most of which are represented in the Australian marine fauna. They are the bubble shells of collectors.

The classification of the Cephalaspidea remains in a state of flux. The arrangement followed here is fairly conservative, based upon the system first proposed by Odhner (1939) but incorporates some of the many additions and refinements of the past 50 years. The somewhat radical classifications proposed by Minichev & Starobogatov (1979a, 1979b) have met with little acceptance.

Superfamily ACTEONOIDEA

Acteonoideans are vermiform, the shell is external, the foot has simple margins, and the mantle cavity and associated organs are directed more or less anteriorly; the external pallial penis is situated just within the mantle cavity, the seminal duct (the vas deferens) is internal, and the nervous system is streptoneurous.

The three acteonoidean families demonstrate an evolutionary sequence. Members of the infaunal Acteonidae can withdraw completely into the heavy shell with its moderately elongate spire and can close the small aperture with the operculum. In the Bullinidae, which are epifaunal, the animal is flamboyant and it too can completely withdraw into its lighter shell; although an operculum is present, it is much smaller than the aperture. In the Hydatinidae, which are also epifaunal, the animal is flamboyant and large; it can only contract, not completely withdraw, into the large globose thin shell, and an operculum is lacking.

The Acteonidae have been postulated as a model for the archetypal opisthobranch (Morton 1958b; Yonge & Thompson 1976), but this is now disputed (Gosliner 1981a). Nevertheless, the heavy shell with operculum, anteriorly directed mantle cavity, and streptoneurous nervous system are all caenogastropod attributes, indicative of their basal systematic position.

Family Acteonidae

The external shell is stout, relatively robust, capacious and fully able to contain the retracted animal (Fig. 16.21). It is usually less than 25 mm in length but reaches almost 50 mm in *Neacteocina* (Dell 1990). The spire is usually prominent, but rarely either elongate or depressed. There can be up to eight whorls. The aperture is narrow, the sinuous columella may have one or more strong folds. The sculpture is spiral and consists of weak to strong punctate grooves. The periostracum is thin. A chitinous operculum usually fills the aperture (seldom present in *Rictaxis*).

The cephalic shield is shallowly bilobed anteriorly, and posteriorly carries two large rounded lobes that protect the neck and front part of the shell (Fig. 16.21A). The eyes may be visible at the medial base of the posterior lobes. The foot is usually broad and short, with angular or tentacular anterior corners, and a tail which is rarely longer than the shell. There are no parapodia. The mantle cavity is more or less anterior with the antero-lateral aperture on the right side. An anteriorly directed plicate gill is present. The penial column, just within the mantle cavity, may be long and prominent, or only a small conical papilla. There is an internal prostate gland and vas deferens, and one (*Acteon*) or two (*Pupa*, *Punctacteon*) female accessory sacs (bursa copulatrix, seminal vesicle). A short oral tube precedes the buccal bulb (pharynx), and there is a little-differentiated oesophageal crop. The jaws are composed of denticulate chitinous rods. The radular row may have a small, oblong median tooth, flanked each side by up to 25 long slender lateral teeth (*Crenilabium*, *Neacteocina*). However, the median tooth is usually lacking, with five to 13 (*Pupa*, *Punctacteon*,

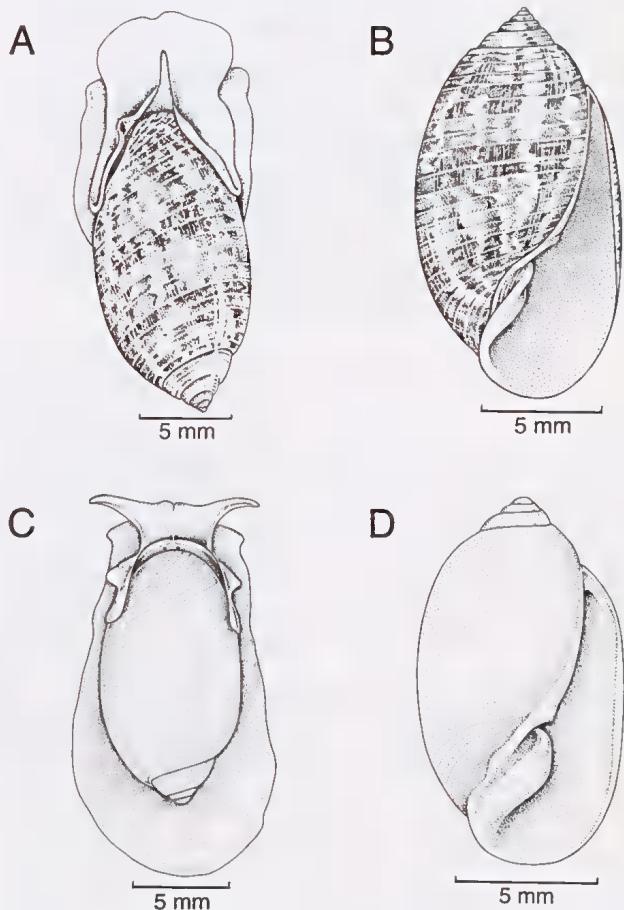


Figure 16.21 Family Acteonidae. A, B, *Pupa sulcata*. C, D, *Pupa nitidula*. A, C, animal, dorsal view; B, D, shell, apertural view. (A, after photograph by W.B. Rudman; C, after sketch by R. Burn) [R. Plant]

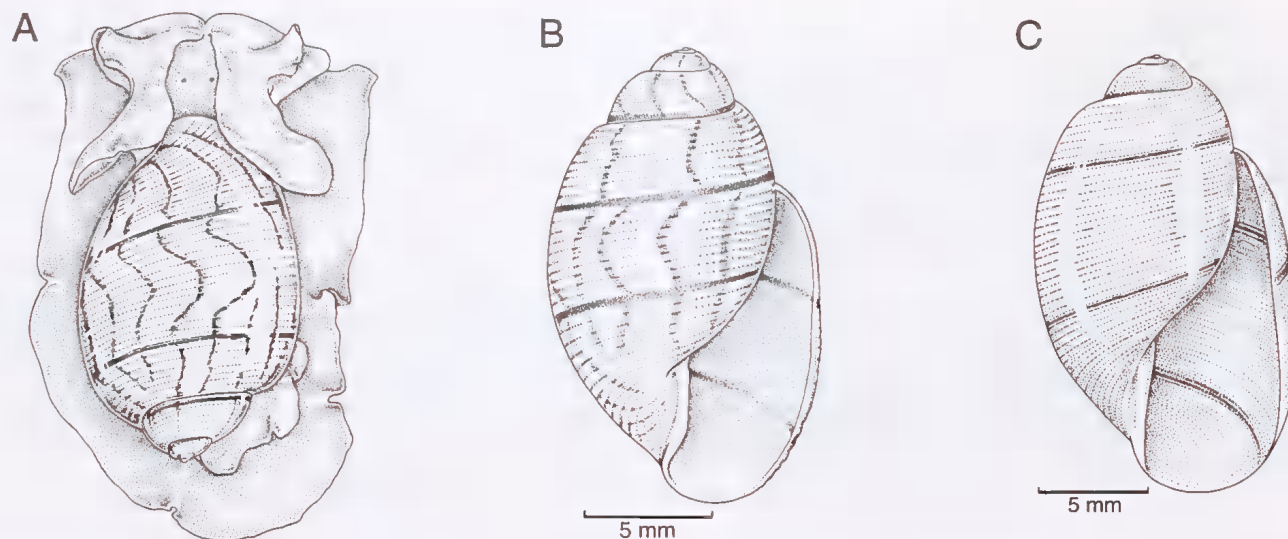


Figure 16.22 Family Bullinidae. A, B, *Bullina lineata*. C, *Bullina melior*. A, animal, dorsal view; B, C, shell, apertural view. (A, after photograph by N. Coleman) [R. Plant]

Rictaxis, *Japonactaeon*) or 36 to 65 (*Mysouffa*, *Inopinodon*) denticulate lateral teeth each side of the centre. In *Acteon*, the teeth are extremely small (less than 20 μm high), denticulate along one edge, and both teeth and rows are extremely numerous. The circumoesophageal nerve collar encircles the inner end of the oral tube, the cerebropleural ganglia are concentrated, the visceral loop is long and partly streptoneurous, with the intestinal ganglia far behind the cerebropleural ganglia and the visceral ganglion as far behind again.

The European *Acteon tornatilis*, now regarded as somewhat anomalous because of its radular characteristics, is by far the best known species in the family through the publications of Bouvier (1893), Pelseneer (1894), Guiart (1901), Perrier & Fischer (1911), Fretter (1939), Fretter & Graham (1954), Johannson (1954) and Hurst (1965). More recently, studies have been made of *Japonactaeon* (Taki 1956), *Acteon pelecais* (Marcus, Er. 1958b) and the Acteonidae of New Zealand (Rudman 1972b, 1971c, 1972h). Acteonids appear to be obligate feeders on polychaete worms; an interesting summary is given by Yonow (1989). Apparently they breed over the summer months (Rudman 1972b; Thompson 1976), and lay elongate club-shaped egg masses anchored by a mucous strand into the sediment (Fretter & Graham 1954). The eggs pass through typical developmental phases to a free swimming veliger (Thompson 1976).

Of the acteonid shells, only those of *Pupa* with heavy double or compound columellar folds (Fig. 16.21B, D) and *Crenilabium* with an elongate slender shell can be recognised easily. The other genera have more or less uniform shell characters but have been separated on differences in the shape and number of radular teeth (Marcus, Ev. 1972a, 1974; Bouchet 1975). Deep-water acteonid shells are generally dull whitish in colour, whereas some of those from shallow waters are strikingly patterned. Among the northern Australian species, *Pupa nitidula* (Fig. 16.21C) is bright pink with a white columella, *P. solidula* has spiral bands of reddish quadrate spots, and *Punctacteon flammea* has bold reddish axial flames.

Acteonids have a very long geologic history, first appearing in the Cretaceous of Europe (Zilch 1959–1960; Gosliner 1981a), and there are many fossil generic and specific taxa. In the Tertiary beds of southern Australia, acteonids including *Crenilabium* are present from the Eocene onwards (Cossmann 1897; R. Burn personal observation). Recent species were reviewed by Pilsbry (1895), and since then have been added to extensively by Thiele (1912, 1925), Habe (1950c) and Lin (1989), among others. Extant species live in a variety of habitats, ranging from sandy areas of the lower intertidal (Fretter & Graham 1954) to depths exceeding 3000 m (Bouchet 1975).

Around Australia, *Pupa* is common in northern shallow waters (Short & Potter 1987), but is taken in dredge samples along the southern coastline. *Punctacteon* is present in northern waters, and *Acteon* has been reported (W.B. Rudman personal communication).

The genus *Leucotina*, long regarded as an acteonid, has recently been transferred to the family Amathinidae in the Pyramidelloidea (Ponder 1987). Several other genera may be misplaced. The cancellate shell and deep posterior sinus of the aperture of *Obrussena* from deep water off New South Wales and Japan (Iredale 1925; Habe 1952; Tsuchida 1991), and the ovoid, almost *Marginella*-like *Ovulactaeon* from the western Atlantic, indicate that both are unlikely to be members of the family.

Family Bullinidae

The circumtropical and subtropical genus *Bullina*, with several, often not well delimited, species, is the only genus in the Bullinidae (Fig. 16.22). The external shell is at most 20 mm in length, well calcified, capacious, with a short or depressed spire, and sculptured with spiral punctate grooves. The aperture is large and rounded in front, and narrower behind (Fig. 16.22B, C). The columella is straight and there is a small umbilicus. The white or cream shell bears red, brown or black spiral bands and axial flames. A thin periostracum is present.

The animal is white (Rudman 1972i) or brightly coloured with pale blue body and a narrow, iridescent, green-blue edge to the foot, cephalic shield and exhalant siphon (Pl. 33.1). It can withdraw completely into the shell. The anterior corners of the large cephalic shield are folded ventrally to form an open funnel each side of which connects to the Hancock's organs. Posteriorly, a pair of large lobes covers the front and sides of the shell (Fig. 16.22A). Small eyes are visible medially between the lobes. The infrapallial lobe projects from the end of the aperture to form a large exhalant siphon. The foot is as broad or broader than the shell, the anterior corners are angular, and the tail broadly rounded. Parapodia are lacking. A thin chitinous operculum is present.

The large mantle cavity opens to the right; the gill is large and plicate. The penis projects as a stout column into the anterior corner of the mantle cavity. The seminal duct is an internal vas deferens to the base of, and within, the penial column with its small terminal papilla. A bursa copulatrix with a duct to the genital vestibule and a proximal seminal receptacle are both present. The alimentary canal has an oral tube, an unpaired oral gland and an oesophageal crop, as well as a muscular pharynx and paired salivary glands. The jaws are composed of triangular elements. The radular row has a small, elongate, rectangular, central tooth, flanked each side by 11 to 18 basally small, triangular teeth with four to seven denticles along the

posterior edge. The nerve collar encircles the oral tube or anterior part of the pharynx, the cerebral ganglia are concentrated, the visceral loop is streptoneurous with the intestinal and visceral ganglia well separated.

The best-known species, *Bullina lineata* (Fig. 16.22A; Pl. 33.1), is a common Indo-West Pacific tropical and warm temperate species (Kay 1979) in intertidal and shallow subtidal waters to a depth of 15 m. It is reported from much of eastern Australia (Allan 1950). Other species are described from Australia (Iredale 1929), New Zealand (Rudman 1971d) and Japan (Habe 1950b). Two tropical western Atlantic species are known (Abbott 1974). The egg mass of *B. lineata* is a cylindrical cord, coiled like a spring (Kay 1979), with one end connected to a long mucous strand anchored in the sandy substratum. The eggs are 67 μm in diameter, and develop through typical veliger stages to metamorphosis (Rose 1985). Rudman (1972i) suggested that *Bullina* captures and ingests polychaete worms, and Taylor (1986) found the remains of sedentary cirriform polychaetes in the gut of Guam specimens. Aspects of the taxonomy and morphology of *Bullina* have been published by Rudman (1971d, 1972i).

Family Hydatinidae

The Hydatinidae are a small family of mostly large, conspicuously coloured species belonging to two or three genera (Fig. 16.23). The shell is external, thin-walled, globose or ovoid, with an exposed nearly level spire, and usually creamish white with spiral (and in *Micromelo* axial) coloured bands (Fig. 16.23B, D). There is a thin periostracum. The aperture is large, the outer lip thin and broadly rounded in front. The smooth columella is curved and the callus extends on to the last whorl. (The name Hydatinidae, retained here for stability since it has long been used, is preoccupied.)

The living animals are flamboyant and often brightly coloured: dull reddish-pink with pale blue margins (*Hydatina physis*); dull purple with white margins (*H. albocincta*); translucent with large white blotches and green and yellow margins to the foot, cephalic shield and exhalant siphon (*Micromelo*). The animal is too large to withdraw completely into its shell.

The cephalic shield is large with a pair of broad posterior lobes (Fig. 16.23A, C); the eyes are visible anteriorly in the groove between the lobes. The anterior edge is folded laterally into two pairs of enrolled lobes below which are the plicate Hancock's organs. A large infrapallial lobe projects from the posterior aperture and folds up around and extends beyond the apex of the

shell. The wide foot has broadly rounded or angular anterior corners, and a broadly rounded tail. Parapodia and an operculum are lacking.

The oral tube is long, with a single posterior oral gland. There is a large oesophageal crop. The jaws are composed of denticulate chitinous rods. The radular row may or may not have a small elongate central tooth with an anterior cusp, flanked on each side by 13 to 21 large triangular teeth each with four to five cusps on the posterior edge. The circumoesophageal nerve ring is situated at the anterior part of the oral tube, the cerebropleural ganglia are concentrated and the supra-intestinal ganglion is attached to the right cerebropleural ganglion. The subintestinal and visceral ganglia may be close together near the posterior part of the long streptoneurous visceral loop, or the subintestinal ganglion might also be far forward, leaving the visceral ganglion isolated.

A closed internal vas deferens leads to the large, projecting penial column at the tip of which is a sheath enclosing a strong penial papilla. The female genital aperture lies beside the base of the penial column, the bursa copulatrix opens through its long duct to the genital vestibule, and the seminal receptacle is proximal. The mantle cavity is large and opens to the right. It contains a large plicate gill.

Hydatina and *Micromelo* species feed on polychaete worms (Bergh 1901; Eales 1938; Rudman 1972a; Gosliner 1987a). Eales (1938) found a cirratulid polychaete 80 mm long and 4 mm wide in the crop of a 15 mm long, preserved *H. velum*. Members of these genera occur in intertidal and shallow subtidal waters, where they crawl about in the open on reefs and sand and seagrass flats. Several species of *Hydatina* occur in Australian seas (Short & Potter 1987). *Micromelo* apparently has only the one species, for a long time known as *M. guamensis* but identical with the Atlantic *M. undata*; it has a shell length of 15 mm and an Australian distribution around the northern coastline. Bergh (1901), Vayssi  re (1906a), Eales (1938) and Rudman (1972a, 1972i) reviewed the morphological characteristics of these two genera, and Pilsbry (1895) the taxonomy of the species.

Mating is reciprocal in *Hydatina physis*. The egg mass is a distinctive, convoluted, spirally twisted white ribbon anchored by one end in the substratum (Baba, Hamatani & Hisai 1956). These authors report finding seven to 16 ova of 57 μm diameter per capsule in Japanese material, whereas there are only one to five ova of 75 μm diameter per capsule in Australian material from Long Reef, New South Wales (Rose 1985). The eggs develop through a veliger stage. The egg mass of *H. amplustre* is smaller and less convoluted (Kay 1979).

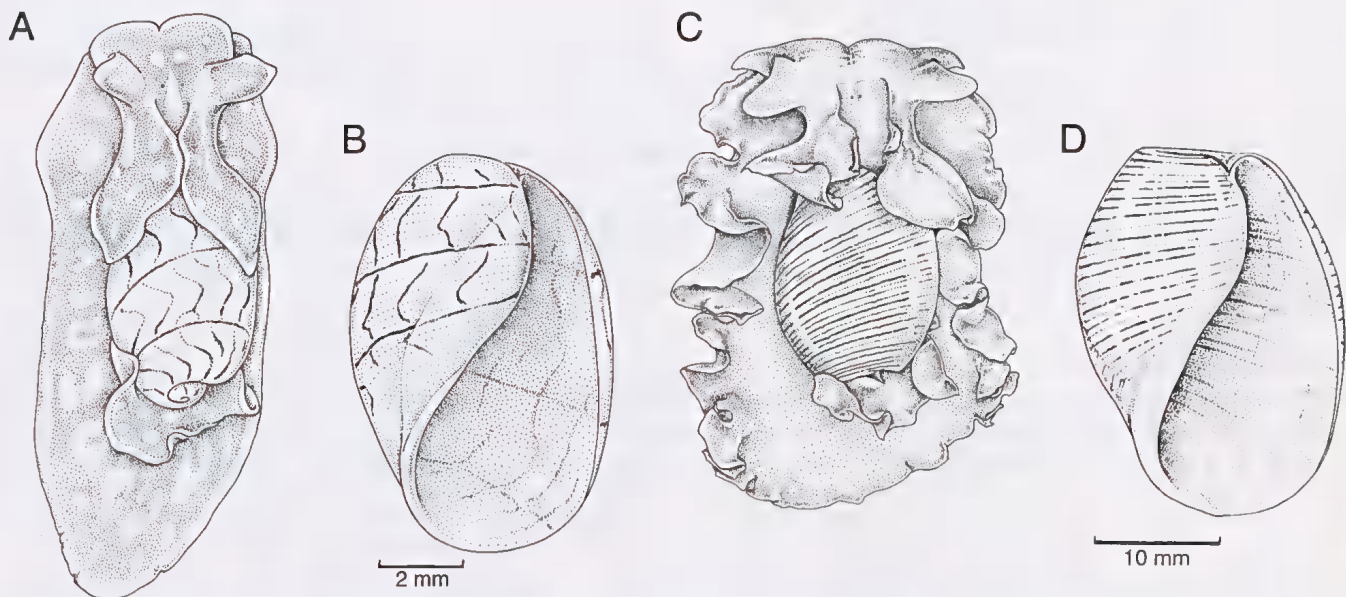


Figure 16.23 Family Hydatinidae. A, B, *Micromelo undata*. C, D, *Hydatina physis*. A, C, animal, dorsal view; B, D, shell, apertural view. (A, C, after photographs by A. Healy) [R. Plant]

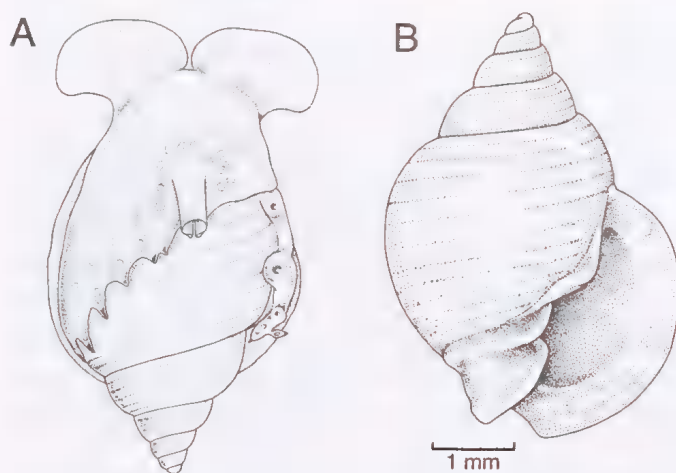


Figure 16.24 Family Ringiculidae. *Ringicula* sp.: A, animal, dorsal view; B, shell, apertural view. (A, after sketch by R. Burn) [R. Plant]

A minute, white, deep-water species from the South Atlantic, *Parvaplustrium tenerum*, has been referred to the Hydatinidae, and in the absence of contrary evidence, seems reasonably placed there. It has a thin, extremely fragile, globose shell less than 3 mm long. The species has been described twice (Powell 1951; Marcus, Ev. & Marcus, Er. 1969a) from waters 71–320 m deep to the north of the Falkland Islands.

The equally small *Noalda exigua*, from the shallow waters of Tasmania, Victoria and New South Wales, has long been associated with the Hydatinidae (Hedley 1902, 1912; Iredale 1936). It is, in fact, an unusual primitive aglajid (Philinoidea) with a relatively big, partly external shell (R. Burn personal observation).

Superfamily RINGICULOIDEA

The Ringiculoidea is apparently a conservative group, in which the shell is quite different from that of other cephalaspideans, and has changed little since the Cretaceous (Zilch 1959–1960). It is thickened and glossy, the columella has one to four strong folds, and the outer lip is generally greatly thickened in the adult. The animals of very few Recent species are known, but these exhibit too few differential characteristics to justify the use of more than one or two generic taxa within the superfamily. Morphologically important features are the lateral fusion of the cephalic shield and foot, the two blade-like lateral teeth in the radular row, the forward-opening mantle cavity, the pre-pharyngeal circumoesophageal nerve ring and the long, euthyneurous visceral loop. The reproductive system varies between species; some exhibit the primitive external seminal groove and others have the more advanced internal closed vas deferens (Gosliner 1981a).

It has been suggested that the living ringiculoids more closely represent the archetypal opisthobranch than do acteonoids (Gosliner 1981a). This view needs to be reassessed when more animals of ringiculoid and acteonoid species have been studied. In a radical move, Minichev & Starobogatov (1979a) transferred the Ringiculidae to their superorder Pyramidelloida as the only family in their order Ringiculida. However, Ponder & Warén (1988) did not include the Ringiculidae as a member of their superfamily Pyramidelloidea.

Family Ringiculidae

The Recent ringiculid fauna is very extensive (Pilsbry 1895; Thiele 1925; Habe 1950a). All species except one (Minichev 1966) have been described solely on shell characters. More than a dozen species are reported from Australian waters, but many of the identifications are doubtful. The anatomy of only four species is known (Pelseneer 1925; Fretter 1960; Minichev 1967; Gosliner 1981a), the radular teeth of several others have been figured (Bergh 1908; Thiele 1925; Habe 1950a; Bouchet 1975; Thompson, Jarman & Zenethos 1985), and there are notes on the live animals of two more (Watson 1878; Annandale & Prashad 1919).

The ringiculid shell is external, glossy, robust, small (usually less than 10 mm long), rounded and conical (Fig. 16.24B). The spire is small, smooth or spirally sculptured, rarely axially ribbed. The aperture is large, but is restricted by either one large columellar fold (*Microglyphis*) or two, three, or four strong columellar folds and a much thicker outer lip (*Ringicula*). There is an anterior apertural sinus.

The animal can retract fully into the shell, and there is no operculum. The short, broad cephalic shield is bilobed and often expanded anteriorly (Fig. 16.24A). Posteriorly it runs obliquely back to the ventral side of the shell, and coalesces laterally with the foot margins to form a sheath-like structure protecting the aperture of the shell. In the active animal, a dorso-medial siphonal fold develops in the posterior margin of the cephalic shield, leading to the anterior apertural sinus. At rest, or when irritated (R. Burn personal observation), the siphonal fold opens out and contracts. The posterior border of the cephalic shield and the lateral edges of the foot bear large defensive glands arranged in one or two rows parallel to the border (Fretter 1960; R. Burn personal observation). Anteriorly, the foot is sinuate and separated by a deep fold from the cephalic shield; laterally it merges with the cephalic shield; and posteriorly it is broadly rounded and shorter than the shell. The body is generally colourless or whitish with scattered white cells and glands, with some brownish marks on the exposed extremities in shallow water species. The eyes are usually hidden deep within the integument or not visible dorsally.

The mantle cavity is directed forward; the gill is simple (Fretter 1960) or plicate (Gosliner 1981a). The buccal bulb has both jaws (with denticulate or indented edges to the elements) and a radula, with generally only one pair of long, smooth, curved, blade-like lateral teeth per row. A minute, bilobed, oblong central tooth has been reported in one species (Thompson *et al.* 1985), and fine denticles along the distal inner edge of the lateral teeth in another (Habe 1950a). There are no gastral plates. The circumoesophageal nerve ring encircles the buccal bulb anteriorly, the central ganglia are concentrated, one or both intestinal ganglia are far forward just behind the cerebral ganglia (Fretter 1960; Minichev 1967), and the visceral ganglion lies isolated near the posterior end of the visceral loop.

The reproductive system has been reported to be androdiaulic in one species (Pelseneer 1925), that is, the male duct divides proximally, has a distinct prostatic section, a closed vas deferens within the body cavity, and terminates in an invaginable penis. In other species it is monaulic (Fretter 1960; Minichev 1967; Gosliner 1981a), with an external seminal groove or tract to the invaginable penis with its prostatic bulbs. There may be a bursa copulatrix with a long duct attached to the genital vestibule, and a proximal seminal receptacle (Fretter 1960; Gosliner 1981a), or only the latter (Minichev 1967).

Ringiculids inhabit temperate and tropical seas. They live in fine-grain sandy areas near algal mats and seagrass beds just below tide level (R. Burn personal observation), down to depths exceeding 5000 m (Minichev 1966). Their ecology and behaviour are known only from laboratory observations of one species (Fretter 1960). Foraminiferans have been found in the gut of two species (Pelseneer 1925; Bouchet 1975), and interstitial copepods in another (Fretter 1960). Ringiculids are preyed upon by aglajid cephalaspideans in Australian waters (R. Burn personal observation). In addition to *Microglyphis* and *Ringicula*, other genera in the family are *Ringiculina*, *Ringiculopsis*, *Pseudoringicula* and *Ringiculinopsis*. Nothing is known of their anatomy or general biology. The small-shelled genus *Pugnus*, long associated with the Ringiculidae, is a marginellid (Maes 1967).

Australian fossil ringiculids appear in the Palaeocene (genus *Avellana*), and *Ringicula* species are common and varied throughout the Tertiary beds of south-eastern Australia (Cossmann 1897; R. Burn personal observation).

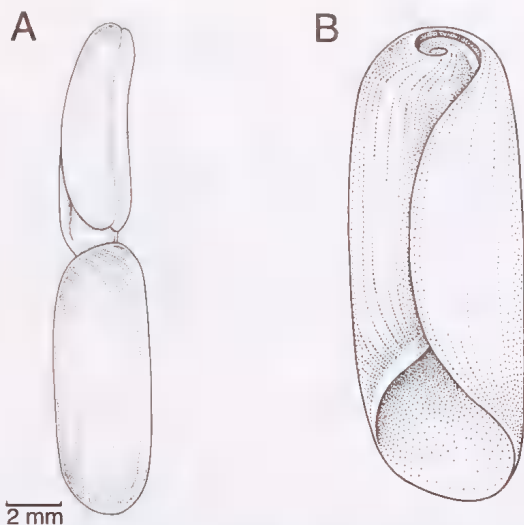


Figure 16.25 Family Cylindrobullidae. *Cylindrobulla* sp.: A, animal, dorsal view; B, shell, apertural view. (A, after sketch by R. Burn) [R. Plant]

Superfamily CYLINDROBULLOIDEA

Cylindrobulloids form a monotypic group of primitive flexible-shelled cephalaspideans (Fig. 16.25) with a small retractable animal, a simple short foot, a uniseriate radula of broad denticulate teeth, an internal vas deferens, a somewhat posterior cephalic penis, a vaginal arrangement of seminal receptacles, and a post-pharyngeal circumoesophageal nerve ring. An operculum, parapodia, Hancock’s organs, jaws and gizzard plates are all absent.

Cylindrobulloids are unique among cephalaspideans because of the thin, fragile, ‘elastic’ shell (Fig. 16.25B) into which the animal can retract, and for the absence of Hancock’s organs at the sides of the cephalic shield. The shell of the anaspidean *Akera* is similar, but the animal is large and very different. The diaphanoidean *Newnsia* has similar but longer radular teeth, and its animal is large and has an external seminal groove. The attachment of both seminal receptacles to the vagina is also unique in these cephalaspideans. This feature also occurs in some species of the notaspidean genus *Berthella* (Ghiselin 1966).

The little that is known of the morphology suggests that cylindrobulloideans arose early in the evolution of the Cephalaspidea (Jensen 1989).

Family Cylindrobullidae

The Cylindrobullidae (Fig. 16.25) are a group of small cephalaspideans which are difficult to distinguish satisfactorily from the morphologically similar snails of the sacoglossan genus *Ascobulla* (Oxynoeoidea, Volvatellidae). Both are found among, and apparently feed upon, green algae of the genera *Caulerpa* and *Halimeda*.

This family has not been found in Australian waters and is not further considered here.

Superfamily DIAPHANOIDEA

The members of this cephalaspidean superfamily have an external shell (except *Colpodaspis*), an external seminal groove, a cephalic penis, a simple foot, a simple ridge-like rear edge to the cephalic shield, a pre-pharyngeal circumoesophageal nerve ring and a median tooth in the radula (except in *Colpodaspis*). At present there is only one family, but it has been suggested (Odhner 1952; W.B. Rudman in Brown 1979) that each constituent genus should be separated as an independent family. Two genera, *Bogasonia* and *Toledonia*, in which some species have a primitive acteonid-like shell, are already placed in a separate subfamily (Warén 1989).

Family Diaphanidae

The diaphanid shell is opaque, rarely more than 5 mm long, thin and fragile, capacious and umbilicate (Fig. 16.26). The spire is slightly raised or depressed. The aperture is widest in front and rounded, the outer lip is sinuous, and the columella has no folds. The white animal is small and retiring, never extending much beyond the shell, and able to retract completely. The cephalic shield is shallowly bilobed in front with the outer corners thickened into small recurved lobes that fold up and out along the edge of the shell. The rear edge of the cephalic shield is confluent over a small ridge with the neck. The eyes are usually prominent dorsally, well back from the front edge and widely spaced, in front of the shell when crawling but usually ‘under the protection of the transparent shell, through which it looks as through a window’ (Alder 1848). The foot is shorter than the shell and wider anteriorly with a sinuous margin; the tail is forked. An infrapallial lobe fills the posterior part of the aperture (Forbes & Hanley 1848–1853; R. Burn personal observation).

The radular row comprises a broad oblong or shallowly bilobed central tooth, sometimes minutely serrate along the upper edge, flanked each side by a large, elongate, cuspidate lateral tooth arising from a narrow base. The invaginable penis is armed with a hyaline or fibrous spine (Bergh 1901; Odhner 1914). The bursa copulatrix is a swelling or pyriform vesicle attached to the lower spermoviduct (Odhner 1926). The mantle cavity opens to the anterior right, and encloses a small gill. The circumoesophageal nerve ring is pre-pharyngeal, the cerebral, pleural and pedal ganglia are concentrated, and the visceral and supra-intestinal ganglia are appressed at the posterior of the very short visceral loop.

True diaphanids, in the subgenus *Diaphaninae*, belong to the genus *Diaphana* (Fig. 16.26A–C). Very few biological data are available for this genus. Specimens are usually sorted out of dredged material from shallow subtidal to continental slope and abyssal waters. *Diaphana minuta* burrows in sand in sublittoral areas around Britain. It spawns in June, and the eggs are 70–80 µm in diameter (Thompson 1976). The best known Australian species is *D. brazieri*, from southern and eastern temperate waters. An almost identical fossil form occurs in the Middle Miocene of Victoria (R. Burn personal observation), and there is a similar species *D. colei*, in southern New Zealand (Powell 1979).

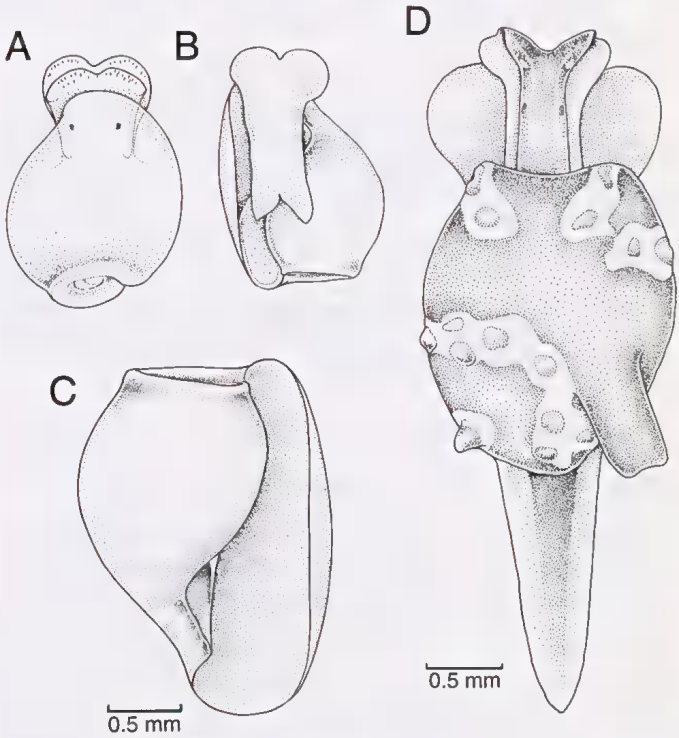


Figure 16.26 Family Diaphanidae. A–C, *Diaphana brazieri*. D, *Colpodaspis thompsoni*. A, D, animal, dorsal view; B, animal, ventral view; C, shell, apertural view. (A, B, after sketches by R. Burn) [R. Plant]

16. OPISTHOBRANCHIA

A separate genus may be required for a group of species which includes the small *D. tasmanica* (shell length 2 mm) from Tasmania and Victoria. This species is sometimes common on turfing brown algae and corallines at low tide. The narrowly cylindrical shell is brownish with a white band. The cephalic shield has a narrow neck and broadly rounded antero-lateral lobes hollowed below. The eyes are prominent at the posterior base of the lobes. The foot is short, widest in front and rounded behind. The sole has a pedal gland just behind mid-length. A small infrapallial lobe projects beyond the shell as a short tail (Burn 1969, personal observation). Several New Zealand species have shells of this kind, and some Antarctic species are similar (Thiele 1912; Powell 1979; Dell 1990).

The epifaunal genus *Colpodaspis* (Fig. 16.26D) has been well documented (Brown 1979), and the tropical Indo-West Pacific species *C. thompsoni* is found in shallow subtidal waters along Australia's northern coastline from North West Cape to the Great Barrier Reef. The shell is internal, thin, bulbous, and shaped like that of *Diaphana*.

The favoured habitat of *C. thompsoni* is among the fronds of species of the brown alga *Turbinaria* (Brown 1979). The north-western European *C. pusilla* is usually found subtidally amongst hydroids and erect bryozoans (Brown & Picton 1979). An associated genus, *Colobocephalus*, from deeper waters off Norway, has a deep sutural sinus in the shell, very short anterior tentacles, and a strong ridge at the rear of the cephalic shield.

The genus *Newnsia* comprises only the Antarctic species *N. antarctica* (Eliot 1906a; Vayssi re 1917; Odhner 1926). The large external shell (to 30 mm), into which the animal can retract almost completely, resembles a thin, very fragile *Hydatina*. *Newnsia* has been dredged in depths of 35–435 m (W gele 1990a).

The subfamily Toledoniinae, with two genera *Toledonia* and *Bogasonia*, includes species with shells very similar to those of the Acteonidae (Marcus, Ev. 1976), and is sometimes placed in that family (Powell 1960; Vicente & Arnaud 1974; W gele 1990a). The external, well-calcified shell has an extended spire and a thickened columella, generally with one fold, which is smooth or spirally furrowed.

Toledonia is primarily an Antarctic and Subantarctic genus, with one species in the far north-eastern Atlantic. It has been found in bottom samples from 9–640 m deep. The 20 named species are not well differentiated (Marcus, Ev. 1976; Dell 1990). The best-known species, *T. limnaeoides* (Odhner 1914; Marcus, Ev. 1976; War n 1989), comes from northernmost Norway, Spitzbergen, Iceland and Greenland. One species, *T. succinaeformis*, has been described from the Auckland Islands, south of New Zealand, and specimens, possibly of this species, have been found in shallow water samples from Macquarie Island (R. Burn personal observation). Further information can be found in Odhner (1914, 1926), Lemche (1948), Marcus, Ev. (1976), War n (1989) and Dell (1990). The newly described *Bogasonia* comes from the seas to the north and north-east of Iceland, in depths of 100–200 m, and there are related Indo-Pacific species (War n 1989).

Superfamily PHILINOIDEA

Philinoideans are carnivorous cephalaspideans with a tendency towards bilateral symmetry, development of parapodia, the rearward displacement and reduction of both mantle cavity and shell, a reduction of jaws, radula, and gizzard plates, and the concentration of central nerve ganglia, shortening of the visceral loop and loss of streptoneury. Thus, the main trends in cephalaspidean evolution are apparent from both the shell and the animal. Rudman (1978) suggested that *Cylichna*, with its heavy shell, total retractability, broad radula, gizzard plates, and partly streptoneurous visceral loop, represents the ancestral form for the superfamily. Gosliner (1980) contended that the relationships are more diverse and complex, but did not suggest a precursorial form. Neither author considered the Retusidae, a

primitive cylichnid-like group which lacks jaws and a radula, or the Philinoglossidae, a highly modified interstitial philinid-like group, as members of the superfamily.

The philinoidean body is divided into the cephalic shield and a visceral hump which may be enclosed in, enclose, or lack, a shell. An operculum is rarely present. The cephalic penis is eversible, a prostate gland is attached to the base, and the seminal groove is external and open. The muscular pharynx generally includes jaws and radula. In the radula, the large lateral tooth has a broad base, a long, curved and twisted cusp, often denticulate along the medial edge, and a broad medial flange. The circumoesophageal nerve ring is pre-pharyngeal and the ganglia are concentrated.

Family Cylichnidae

The family Cylichnidae (= Scaphandridae) includes species that retain many primitive features (Fig. 16.27; Rudman 1978; Gosliner 1980). The anatomy of only a few species is known, though dead shells are quite common in beach and deep water samples.

The shell is strongly calcified, external, and may have a thin brownish periostracum. In the typical genus *Cylichna*, and in *Adamnestia* and *Austrocylichna* (Fig. 16.27B, D), the shell is cylindrical, with a long narrow aperture which broadens anteriorly, and the spire is depressed below the apex of the shell. The shells of *Acteocina* and *Tornatina* (Fig. 16.27E, G) are also cylindrical, but the apex projects as a moderate spire. In the '*Bulla*' *semilaevis* group, the shell is ovoid shell with a sunken spire. *Scaphander* and *Meloscapander* have large, elongate, pyriform to globose shells, the aperture large; the spire is sunken in *Scaphander* and short in *Meloscapander*. Most shells are smooth or finely spirally striate, but in *Scaphander*, *Meloscapander* and *Paracteocina*, the sculpture comprises punctate grooves. Adult shells vary in length from 2–3 mm in *Cylichna*, *Acteocina* and *Tornatina*, to 40 mm in *Scaphander*.

The cylichnid animal is generally small and capable of complete retraction into the shell (Fig. 16.27A, C, E), except in *Scaphander* which contracts only into the aperture. The cephalic shield is short with a pair of posterior lobes. The Hancock's organs are cuticularised. The short foot lacks parapodia. An operculum is present only in '*Bulla*' *semilaevis* (Gosliner 1980). The mantle cavity opens on the right side, and contains a large, plicate gill. The external seminal groove leads to an invaginable cephalic penis. The infrapallial lobe is rarely developed to extend beyond the shell.

Generally the alimentary tract lacks jaws, though they are present in '*Bulla*' *semilaevis*, *Cylichna* and some *Acteocina* species. The radular row usually has a median tooth, which is bilobed and denticulate in *Cylichna*, *Acteocina* and *Tornatina*, and winged or medially concave in *Scaphander*, *Meloscapander* and *Paracteocina*. It is absent in *Adamnestia*, *Cylichnium* and *Mamillocylichna*. A large curved, generally denticulate, lateral tooth with a wide inner flange to the broad base flanks each side of the median tooth and there may be a further two to 10 generally smaller smooth marginal teeth on each side. The three, rarely two, gizzard plates in the muscular gizzard are equal in size and shape, or in some genera very nearly so; plates are lacking in '*Bulla*' *semilaevis* and *Adamnestia*. In *Adamnestia arachis*, the cuticular lining of the gizzard bears raised bosses and ridges (R. Burn personal observation). The gizzard plates are calcified in the larger genera such as *Scaphander*, chitinous in the others.

The circumoesophageal nerve ring encircles the oral tube in front of the pharynx, the cerebropleural ganglia are concentrated and the visceral loop is long and only partly streptoneurous. The visceral and subintestinal ganglia are very close, even fused together, and the supra-intestinal ganglion is little distance away. The penis usually bears a prostate gland and penial papilla, often with unarmed or armed soft papillae which line the penial stem and walls of the penial sheath (*Scaphander*, *Meloscapander*). The bursa copulatrix has a long duct to the genital vestibule, and the seminal receptacle branches off the spermoviduct proximally, or is only a fold of the proximal spermoviduct.

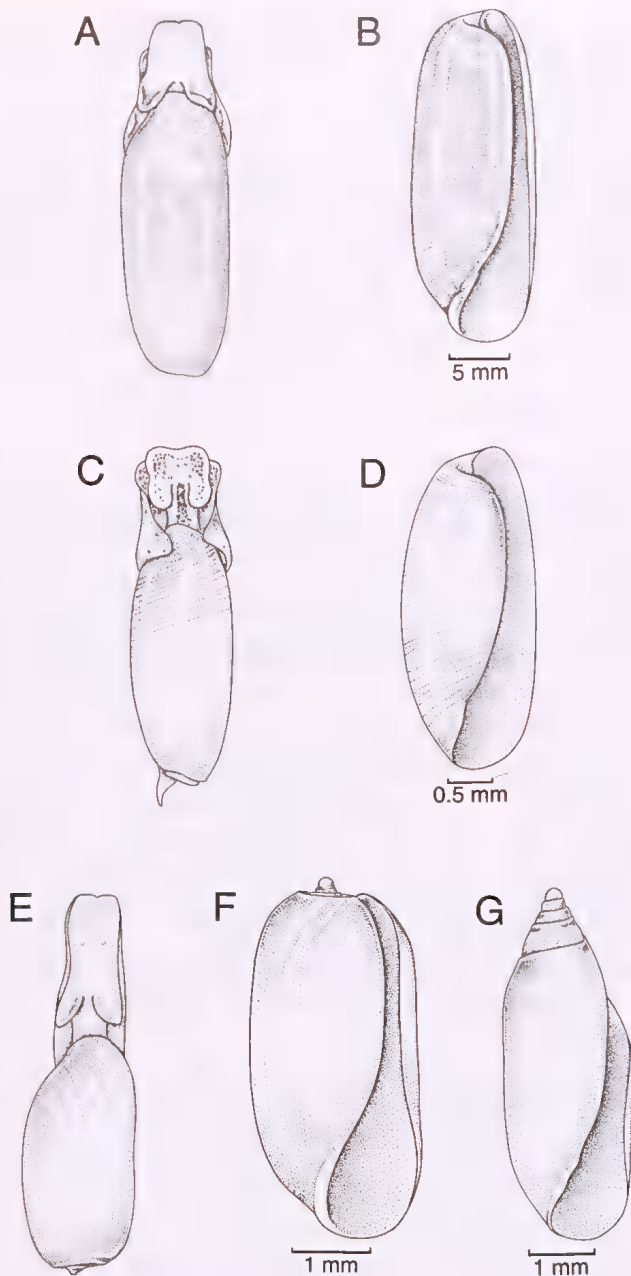


Figure 16.27 Family Cylichnidae. A, B, *Adamnestia arachis*. C, D, *Austrocylichna exigua*. E, F, *Tornatina apiculata*. G, *Tornatina* sp. A, C, E, animal, dorsal view; B, D, F, G, shell, apertural view. (A, C, E, after sketches by R. Burn) [R. Plant]

Cylichnids occur from the intertidal to depths exceeding 5500 m. All species are infaunal and inhabit the top centimetre or so of soft muddy substrata, at least in shallow waters, usually near seagrass beds in protected and semi-protected areas of coastline. Some small species live in the sediment filling the interstices of coralline algae. They are a particularly common component of the shallow benthos of Australia, where species of *Tornatina* are more prevalent than other genera. *Tornatina apicina* and *T. hofmani* are commonly found species in south-eastern Australia, and *T. apiculata* occurs in southern Western Australia.

Adamnestia arachis lives in the shallow subtidal to a depth of 100 m, at least around southern Australia. It may have a dark brown periostracum and grow to 30 mm or more in length. *Cylichna thetidis*, which generally seems to live in deeper waters, has a broad southern distribution, extending to New Zealand, where it is not uncommon in shallow waters (R.C. Willan personal communication). *Scaphander* is represented by only *S. illecebrosus* (Iredale 1925) from deep waters off southern New South Wales, and *S. otagoensis* from New Zealand (Dell 1956). *Meloscaplander* has been found in the seas to the near north of Australia (Schepman 1913).

The '*Bulla*' *semilaevis* group is represented in southern Australia by *Bulla incommoda* and *Austrocylichna lagena* (Smith, E.A. 1891; Burn 1978) and in New Zealand by *Cylichna bulloidea* (Dell 1956). This group of species probably belongs to the East African genus *Sphaerocylichna* (Theile 1925). *Cylichnium* is represented in the Australian fauna by '*Bulla*' *ordinaria* (Smith, E.A. 1891). *Decorifer*, recently re-collected alive from its type locality on Elizabeth Reef, north of Lord Howe Island, is probably a cylichnid close to *Tornatina*.

The genera *Sabatina*, *Nipponscaphander*, *Eoscaplander*, *Bucconia*, *Semiretusa* and *Eocylichna* are also assigned to the family, but neither they nor *Paracteocina* and *Mamillocylichna*, have been found in Australian waters. Fossil cylichnids are common in Australia, with numerous genera and species occurring in the Eocene to Pliocene beds of the southern part of the continent. Elsewhere, cylichnids first appeared in the Jurassic of Europe (Zilch 1959–1960).

The relatively large, more readily available European species, *Scaphander lignarius*, has been the subject of several classical studies (Sars 1878; Vayssi re 1880; Pelseneer 1894; Bergh 1901; Guiart 1901; Perrier & Fischer 1911); congeners have been studied more recently by Fretter (1939), Lloyd (1952), Ev. Marcus & Er. Marcus (1967a), Ev. Marcus (1974) and Bouchet (1975). Lemche's (1956) monumental treatise on *Cylichna* described the anatomy and histology of four European species. *Acteocina* was examined in detail by Er. Marcus (1957), and subsequently by Gosliner (1979) and Mikkelsen & Mikkelsen (1984, 1987). *Tornatina* was reviewed by Ev. Marcus (1977), and *Paracteocina* and *Meloscaplander* were described by Minichev (1966, 1967). The only knowledge of *Cylichnium* and *Mamillocylichna* comes from Bouchet's studies (1975) on the abyssal cephalaspideans of the north-eastern Atlantic.

Little ecological, behavioural or life-history information is available. *Acteocina* and *Cylichna* ingest foraminiferans, both incidentally (Hurst 1967; Bazas & Carle 1979) and selectively (Shonman & Nybakken 1978). *Scaphander lignarius* eats foraminiferans, annelids, scaphopods, bivalves, gastropods, echinoderms and crustaceans (Thompson 1976). The spawn of *Acteocina* is a small gelatinous balloon of eggs attached by a mucous thread to the substratum (Marcus, Er. 1958b), from which veligers emerge and metamorphose (*A. canaliculata*) or benthic juveniles crawl (*A. atrata*) (Mikkelsen & Mikkelsen 1984).

Family Retusidae

A family of small to minute infaunal species with a shell length rarely exceeding 10 mm (Fig. 16.28), the Retusidae live in all seas from the shallowest intertidal sand and mud flats to bathyal depths greater than 5000 m (Minichev 1966). The shell is cylindrical or pear-shaped (*Retusa* – Fig. 16.28B, *Pyrrunculus*, *Relichna*), or posteriorly acuminate (*Volvulella* – Fig. 16.28D), with a long aperture which widens anteriorly. The posterior end of the shell is often truncate, and the protoconch, usually sunken, may be produced into a short, mamillate spire. The shell is usually smooth, but axial or spiral sculpture, or both, may be present.

The cephalic shield is shallowly sinuate in front and produced into two lobes posteriorly (Fig. 16.28A, C). The eyes are hardly visible dorsally. The Hancock's organs are small and lightly cuticularised. The short, broad foot has no parapodial lobes. A small oval chitinous operculum is present in some species of *Retusa* (Minichev 1966, 1971; Burn & Bell 1974b; Luque 1983), but does not fill the aperture. The infrapallial lobe fills the posterior aperture but does not protrude. The gill is a triangular lobe in *Retusa* and *Volvulella* and absent in *Relichna*. The unarmoured, invaginable penis may bear one or two prostate glands as well as a seminal vesicle (Marcus, Ev. & Marcus, Er. 1960; Minichev 1967, 1971; Rudman 1971e; Burn & Bell 1974a, 1974b; Thompson 1976). There is an external seminal groove. The bursa copulatrix is attached by a long duct to the common genital vestibule and is close to the smaller seminal receptacle in

16. OPISTHOBRANCHIA

Retusa (Minichev 1971) or nearer the inner end of the spermoviduct in *Relichna* and *Volvulella* (Marcus, Ev. & Marcus, Er. 1960; Rudman 1971e).

The alimentary tract has neither jaws nor radula. Three oval gizzard plates, one usually larger than the others, are present in the muscular part of the mid-gut behind the soft, distensible crop (except in *Volvulella*; Marcus, Ev. & Marcus, Er. 1960). The plates are composed of tightly packed chitinous rods, and form a smooth concave surface in *Relichna* (Rudman 1971e; Bouchet 1975), or two raised conical points in *Pyrunculus* (Thiele 1925; Habe 1950a; Bouchet 1975), or a field of conical points in *Retusa* (Minichev 1967; Burn & Bell 1974a, 1974b). The circumoesophageal nerve ring encircles the oral tube in front of the pharynx, and the visceral loop is streptoneurous; the intestinal and visceral ganglia are close together.

The western European *Retusa obtusa* is the best-studied species (Hurst 1965; Smith, S.T. 1967a, 1967b; Thompson 1976). It lives below the surface of intertidal and subtidal muddy sand flats, and inhabits only the top few centimetres. It has an annual life-cycle. Copulation takes place in autumn and spawning occurs in the spring months. Each individual lays at most 50 eggs in one to four small gelatinous masses. The eggs are 245–330 µm in diameter. Development is direct to a crawling stage, approximately 28 days after spawning, and the newly hatched juveniles more than double their shell length in 2–3 weeks. Another European species, *R. truncatula*, spawns small egg masses containing 700 or more eggs, 100 µm in diameter. This species has planktotrophic development.

Diatom skeletons have been found in the intestine of *Volvulella* (Marcus, Ev. & Marcus, Er. 1960). The other retusid genera forage for, and eat, foraminiferans and small molluscs (Hurst 1965; Marcus, Ev. & Marcus, Er. 1969a; Rudman 1971e; Thompson 1976). Analyses of gut contents of two southern Australian species (Burn & Bell 1974a, 1974b) showed that *Retusa* species are highly selective in their feeding. Other taxa may also be selective feeders: the crop of *Relichna murchisoni* contained only the foraminiferan *Notorotalia* (Rudman 1971e). *Retusa* species can be extremely abundant in intertidal and shallow subtidal waters when the habitat is suitable and are preyed upon by aglajid opisthobranchs (Burn 1974a).

The shells of *Volvulella* have been reviewed (Harry 1967), but almost nothing is known of the animal, except for one study by Ev. Marcus & Er. Marcus (1960). *Pyrunculus* remains unstudied except for the gizzard plates. The retusid gizzard plates are used for abrading the food, not crushing it as in cylichnids.

All four genera are known from the seas surrounding Australia, but specific taxa and their distributions are poorly known. The older literature shows confusion between *Retusa* (without a radula) and *Tornatina* and *Acteocina* (with a radula) and this can be resolved only by examination and comparison of type series

and living topotypical material. Retusids are common as Middle Miocene and later Tertiary fossils in southern Australia, but are often confused with cylichnids.

The Retusidae are possibly an early offshoot of the lineage that gave rise to the Cylichnidae. The two families are very similar, though easily separated by the presence or absence of jaws and radulae. Differences (probably related to their suctorial habits and food specialisations) also occur in the chemical and mineral composition of the shells of these two groups; retusid shells are softer and thinner than those of cylichnids. Shell matrix protein studies (Ghiselin, Degbens, Spencer & Parker 1967) might throw some light upon their early relationships.

Family Philinidae

The Philinidae (Fig. 16.29) represent a stage in the evolutionary trend among philinoideans towards a fragile, internal shell. Only in *Philine denticulata* is the shell external, and then not completely so. The cylindrical or dorsally flattened animal is large compared to the shell, and cannot retract into it (Pl. 33.3). Several species grow to 100 mm in length, and the shell of *P. angasi* can reach 40 mm in length (Kuroda, Habe & Oyama 1971; Rudman 1972e; Burn 1984; Gosliner 1987a). The cephalic shield is large, often medially grooved, broad in front and tapering bluntly or truncate behind (Fig. 16.29A). The eyes are rarely visible dorsally. The visceral hump is generally longer and higher than the cephalic shield, and posteriorly is either truncate or produced into a simple or multilobed frill. The mantle cavity is posterior and almost ventral, opening to the right and containing a plicate gill. The external seminal groove runs from the mantle cavity forward to the invaginable, cephalic penis to the right of the mouth. Brownish Hancock's organs are present in the lateral groove separating the dorsal and ventral surfaces, and there are two sensory patches on each side of the mouth (Hurst 1965). The foot is large, not longer than the body, and the lateral margins are thickened and raised into strong parapodia.

The living philinid animal is generally white, pinkish white, cream, pale yellow or pale brown, sometimes with flecks of dark brown, red or white. Recently, a uniformly red-orange species and a cream species with transverse dark brown bands have been described from the Indo-West Pacific (Gosliner 1988; Baba 1990).

The internal shell ranges in length from 2–40 mm. It is weakly calcified, whitish in colour, ovate to elongate in shape, of very few whorls and with a greatly dilated aperture (Fig. 16.29B). It is often smooth, but a number of species have weak to strong spiral, catenoid or punctate groove microsculpture.

The strongly muscular, often eversible, pharynx lacks jaws. The radular row rarely has a small, somewhat caducous, median tooth. All philinids have a pair of large, curved, lateral teeth which are generally denticulate on the inner side, and there may be an additional one to six smaller, smooth marginal teeth. The gizzard

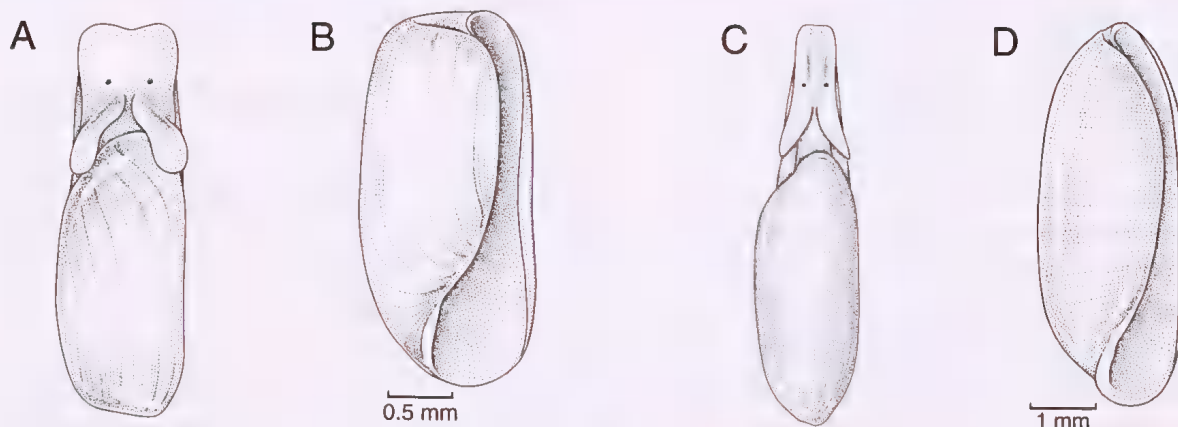


Figure 16.28 Family Retusidae. A, B, *Retusa pelyx*. C, D, *Volvulella rostrata*. A, C, animal, dorsal view; B, D, shell, apertural view. (A, C, after sketches by R. Burn)

[R. Plant]

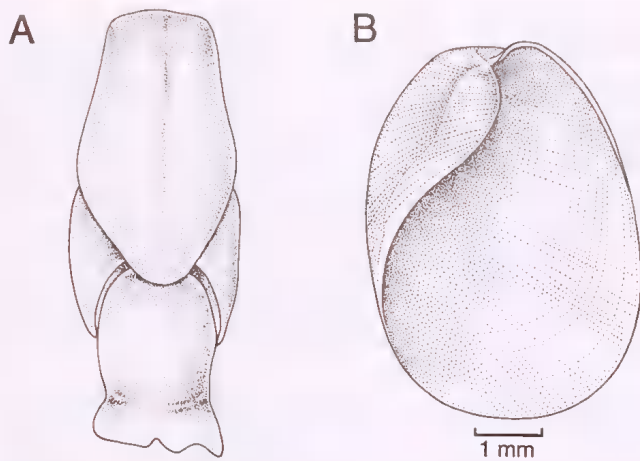


Figure 16.29 Family Philinidae. *Philine columnaria*: A, animal, dorsal view; B, shell, apertural view. (A, after sketch by R. Burn) [R. Plant]

usually contains three large, uneven calcareous gizzard plates, but these may be smaller and chitinous, or lacking altogether. The gizzard may have a cuticular lining raised into longitudinal ridges (Gosliner 1988) in place of gizzard plates.

The circumoesophageal nerve ring lies before the pharynx and the cerebropleural ganglia are concentrated. The visceral loop is long, short or very short, euthyneurous – with a posterior trace of streptoneury in *Philine aperta* (Guiart 1901), the supra-intestinal ganglion is situated at varying distances from the right cerebropleural ganglion, and the subintestinal and visceral ganglia may be joined or slightly separated at the posterior end of the visceral loop (Rudman 1972e; Gosliner 1988).

The penis is simple or complex. Generally a penial papilla with a bulbous, cylindrical or tubular prostate gland at the base is present. There may be a separate sperm bulb, or a separate exogenous sperm duct and long winding ejaculatory duct (Rudman 1972e; Marcus, Ev. 1974). Both the bursa copulatrix, attached to the genital vestibule, and the seminal receptacle, attached to the proximal spermoviduct, are present.

The larger philinids are known to copulate in pairs in line (Guiart 1901), with the one behind fulfilling the male role. The spawn is a rounded or elongate gelatinous balloon anchored by a mucous thread into the substratum (Horikoshi 1967; Challis 1969b; Rudman 1972e) from which free-swimming veligers emerge. The operculum is lost at metamorphosis. The Antarctic *P. gibba* emerge as non-pelagic, crawling juveniles, after the slow-growing embryos break free of the capsules and spawn balloon, some 120 days after spawning (Seager 1979). The Japanese *P. japonica* has a free-swimming veliger that emerges 13–16 days after spawning (Hamatani 1961).

Philinids generally inhabit soft muddy-sand substrata where they plough through the top few centimetres in search of food. The New Zealand *Philine auriformis* burrows 150 mm under the surface (Rudman 1972f). Some small species are strictly epifaunal (R. Burn personal observation). Apparently all philinids are carnivorous. The European *P. aperta* actively seeks out foraminiferans, small gastropods and bivalves, echinoids, and polychaetes in the genus *Pectinaria* (Hurst 1965). *Philine angasi* and *P. auriformis* from New Zealand eat bivalves, the former *Austrovenus stutchburyi*, the latter *Nucula hartvigiana* (Rudman 1972f). In Hong Kong waters, *P. orientalis* has a broad but mostly molluscan diet (Taylor 1982); it prefers juveniles of the bivalve *Tapes philippinarum* during the inshore breeding season (Morton & Chiu 1990). The Japanese *P. japonica* feeds mainly on a variety of bivalves but also on crustaceans, echinoderms and fish remains (Hamada & Ino 1957). On the other hand, the same species has been found with the gut mainly full of little cylichnids (*Decorifer*) along with small bivalves and sometimes even small specimens of its own kind (Hamatani 1961). Other species have been reported to have foraminiferans and stones among their gut contents (Marcus, Ev. 1974).

Various morphological aspects of the nervous, reproductive and alimentary systems of *P. aperta* have been studied by Vayssi re (1880), Guiart (1901), Brown (1934), Fretter (1939), Lloyd (1952) and Hurst (1965). These have been complemented by studies of other species by Challis (1969b), Rudman (1972e, 1972f), Ev. Marcus (1974), Bouchet (1975) and Gosliner (1988). The reproductive biology of five species only has been reported (Hamatani 1961; Horikoshi 1967; Seager 1979). Population structure and growth are described by Horikoshi (1967) and Seager (1982).

The diversity of shell shape and sculpture has led to a number of subdivisions of the primary genus *Philine*. However, anatomical features transcend these subdivisions (Rudman 1972f; Gosliner 1988) because there are many intermediates. When sufficient anatomical data from a wider range of species are available, it might be possible to segregate generic units, for which the names *Hermania*, *Ossiania*, *Johania*, *Rhinodiaphana*, *Philingwinea*, *Retusophilina* (all European) and *Philinorbis*, *Chosophilina*, *Globophilina*, *Yokoyamaia*, *Pseudophilina*, *Laona* (all Japanese) are available. In most of these taxa, only the shell and, rarely, the gizzard plates are known, whereas almost nothing is known about the nervous system.

Spiniphiline, a small white philinid from the Indian Ocean, has been separated recently from *Philine* because it has a shell with long posteriorly directed spines, a gizzard with two elongate plates and a small discoidal plate (as in some *Tornatina*), and a very short visceral loop which terminates near the middle of the body rather than far behind (Gosliner 1988).

The large *Philine angasi* (Pl. 33.3) is common and widespread throughout southern Australia and northern New Zealand. It lives in the top few centimetres of fine silty sand in protected bays, and in deeper water to at least 100 m. *Philine columnaria* (Fig. 16.29A) is common subtidally, and at times among exposed *Zostera* beds in south-eastern Australia. The small, brown-banded *P. orca* is found in shallow subtidal waters of Queensland and Northern Territory (R. Burn personal observation). An animal of the *Pseudophilina*-type has been found in deep-water samples off New South Wales and South Australia (Hedley 1902, 1903, 1907; Verco 1909). Philinids are quite common in the Tertiary beds of southern Australia (R. Burn personal observation) but to date none has been described. Some species' lineages are apparent, with links to extant species found along the eastern seaboard. The first philinids appeared in the Cretaceous (Zilch 1959–1960).

Family Philinoglossidae

Only seven species distributed among four genera constitute this family of small worm-like cephalaspideans (Fig. 16.30). They are adapted to an almost wholly interstitial life. The smooth unpigmented body is up to 3.5 mm in length, elongate and three to six times longer than wide. A shell is absent, or is vestigial and internal in the posterior end of the dorsal surface.

Philinoglossids are rarely found due to the collecting methods that are needed, and the difficulties of recognising them for what they are. They are interstitial, occurring together with acochlidean opisthobranchs. Challis (1969b, 1969c) treated in some detail, the composition and ecology of organisms in this habitat, as well as methods required for their collection. Excellent descriptions of habitats and species have been given by Er. Marcus (1953, 1959), Ev. Marcus & Er. Marcus (1954, 1958) and Salvini-Plawen (1984), and the whole family was briefly reviewed and figured by Arnaud, Poizat & Salvini-Plawen (1986). Spawning and veliger development, typically philinid, are known only for *Philinoglossa helgolandica* (Swedmark 1968).

Most philinoglossid species have been described from the Atlantic and Mediterranean. There are no known Australian records. There is one Red Sea species *Sapha amicorum*, and *P. marcusii* (Fig. 16.30) has been described from localities in the Solomon Islands (Challis 1969a).



Figure 16.30 Family Philinoglossidae. *Philinoglossa marcusii*, dorsal view. (After Challis 1969a) [R. Plant]

Family Aglajidae

Aglajids are specialised philinoideans (Fig. 16.31) united by the presence of sensory bristles beside the mouth, the yellow gland in the mantle cavity and by the absence of jaws, radula (except in *Odontoglaia*) and gastral plates. The large, cylindrical body is divided into an anterior cephalic shield and posterior visceral hump (Fig. 16.31A–C; Pl. 33.2). The cephalic shield is generally triangular, and the broader anterior edge may be lobed with the lateral corners folded into sensory siphons (Fig. 16.31C, F) directing water over the Hancock's organs. The narrower posterior lobe lies over the anterior part of the visceral hump, or is raised vertically (*Philinopsis*). The visceral hump is elongate and ovoid, and posteriorly projects into a terminal multilobed frill or elongate tapering caudal lobe or lobes. The parapodia are long and well-developed laterally.

The reduced shell, somewhat like the apical part of a *Bulla* shell, fills most of the shell cavity. It is well calcified in *Chelidonura* and *Noalda*. In the other genera, the shell has a narrow to wide membranous wing beyond the weakly calcified apical shoulder of the whorls. The shell is generally translucent to white, except in *Chelidonura* in which it is reddish-brown. The shell in *Noalda* (Fig. 16.31E) is typically bulloid, partly external, and white in colour with one or two reddish-brown spiral bands (Hedley 1912; R. Burn personal observation).

Living animals vary in colour from black, through grey, brown, blue, green, orange, yellow to white, often with striking specific combinations of colours (Pl. 33.2; Baba 1949; Coleman 1975; Gosliner 1987a).

The mantle cavity opens ventrally in the right posterior quarter of the visceral hump, and contains the laterally directed gill. A long, external seminal groove extends along the right side from the mantle cavity to the cephalic penis. Only *Odontoglaia* has a radula, consisting of a pair of large curved lateral teeth with one side denticle in each radular row. All other aglajids have a strongly muscular pharynx, eversible in most genera, and a large distensible crop, both bereft of hard parts.

The pre-pharyngeal circumoesophageal nerve ring has concentrated cerebropleural ganglia and a short or very short cerebral commissure. The supra-intestinal ganglion is fused to the right pleural ganglion, and the subintestinal and visceral ganglia are fused at the end of the long, euthyneurous visceral loop. The penis bears a conical or blade-like penial papilla, and one or two prostate glands. The bursa copulatrix and seminal receptacle both open to the genital vestibule, though the latter may open proximally to the spermoviduct. In some genera, a fibrous muscular diaphragm separates the organs of the head cavity beneath the cephalic shield from the viscera within the visceral hump (see Fig. 16.8; Rudman 1974).

Aglajids are active predators (Paine 1963; Rudman 1972d). *Navanax* and *Philinopsis* species both seek and eat opisthobranchs, particularly cephalaspideans (Gosliner 1980); and *Melanochlamys*

cylindrica feeds on polychaetes and nemerteans (Rudman 1972d). *Chelidonura hirundinina* has been observed to evert its pharynx and suck up small flat worms (Gosliner 1987a). Nothing is known of the food of the other genera. *Navanax inermis*, from the American Pacific coast, reaches a length of 225 mm and is the giant of the family (Behrens 1980), but many species are less than 10 mm long. The spawn is an elongate gelatinous balloon anchored in the substratum by a mucous thread (Hurst 1967). Many eggs are produced, numbering up to 22 in each capsule depending upon the species and the size of the specimen. The eggs of *Philinopsis giglioli* hatched as free-swimming veligers 10–12 days after spawning (Hamatani 1961). Nothing is known of the embryonic development of other species.

Early studies (Vayssi re 1880; Bergh 1893a; Pelseneer 1894; Guiart 1901) dealt fairly well with the morphology of the larger Mediterranean and North American aglajids. Recent studies (Marcus, Ev. & Marcus, Er. 1960; Rudman 1974, 1978; Gosliner 1980) have evaluated generic criteria, but without total agreement. Nevertheless, these and other studies have greatly advanced the state of knowledge of species from various parts of the world. Rudman (1972c, 1972j, 1973) revised species of the genera *Melanochlamys*, *Philinopsis* and *Chelidonura* (Pl. 33.2), and added the radulate *Odontoglaia* in 1978. Gosliner (1980) revised the species of all the genera and provided lengthy synonymies. Baba (1985) gave anatomical data for *Nakamigawaia*, and Gosliner (1988) added further information on *Chelidonura*. The nomino-typical genus, *Aglaja*, is relatively poorly differentiated.

The tracking behaviour and the chemical composition of the alarm pheromones produced by the yellow gland of *Navanax inermis* have been the basis of a large and interesting series of research papers by Paine (1963), Blair & Seapy (1972), Murray & Lewis (1974), Sleeper, Paul & Fenical (1980) and Beeman & Williams (1980).

More than 60 aglajid species are recognised worldwide. The family is not known as fossils. The genera *Chelidonura*, *Melanochlamys*, *Noalda*, *Odontoglaia* and *Philinopsis* are all represented in the Australian fauna. *Navanax* is best known from the Americas and the Atlantic (Gosliner 1980), and *Nakamigawaia* is presently known only from Japan (Baba 1985). *Pseudophilina*, once thought to be an aglajid, is now placed in the Philinidae because it has a typical philinid body and radula (Kitao & Habe 1982).

Large and small aglajids are common all around Australia and its offshore islands (Adams & Adams 1854; Angas 1867; Verco 1909; Allan 1933, 1950; Burn 1957a, 1966a, 1969, 1989; Rudman 1970, 1972c, 1972j; Coleman 1975; Wells & Bryce 1986; Wells, Bryce, Clark & Hansen 1990), from shallow waters to over 200 m deep (*Philinopsis taronga*; R. Burn personal observation).

Family Gastropteridae

Prior to 1960, this family (known to SCUBA divers as bat-wing slugs) contained only one genus and five species worldwide. Since then three genera and 25 species have been added, and more species await description. Gastropterids are highly developed philinoideans in which the shell is reduced and internal, or absent (Fig. 16.32). When present, the shell, may be either small, calcified, haliotiform, and positioned over the viscera, or very small, fragile, and attached to the posterior coil of the visceral mass. One common deep-water species from eastern Bass Strait has a large, fragile, external shell, like that of the limacinid thecosome *Limacina inflata* (Fig. 16.61A), enclosing the whole visceral mass (R. Burn personal observation).

The body is divided into a cephalic shield and visceral hump. The cephalic shield is short and triangular, with a posterior medial siphon raised and recurved forward over the shield (Fig. 16.32B). The siphon may be supported by a medial rib, the tip of which may project beyond the siphon. The visceral hump is large, elongate and ovoid, with a right lateral ridge representing the upper free margin of the mantle cavity. The ridge may extend somewhat diagonally backwards across the visceral hump and terminate in a short

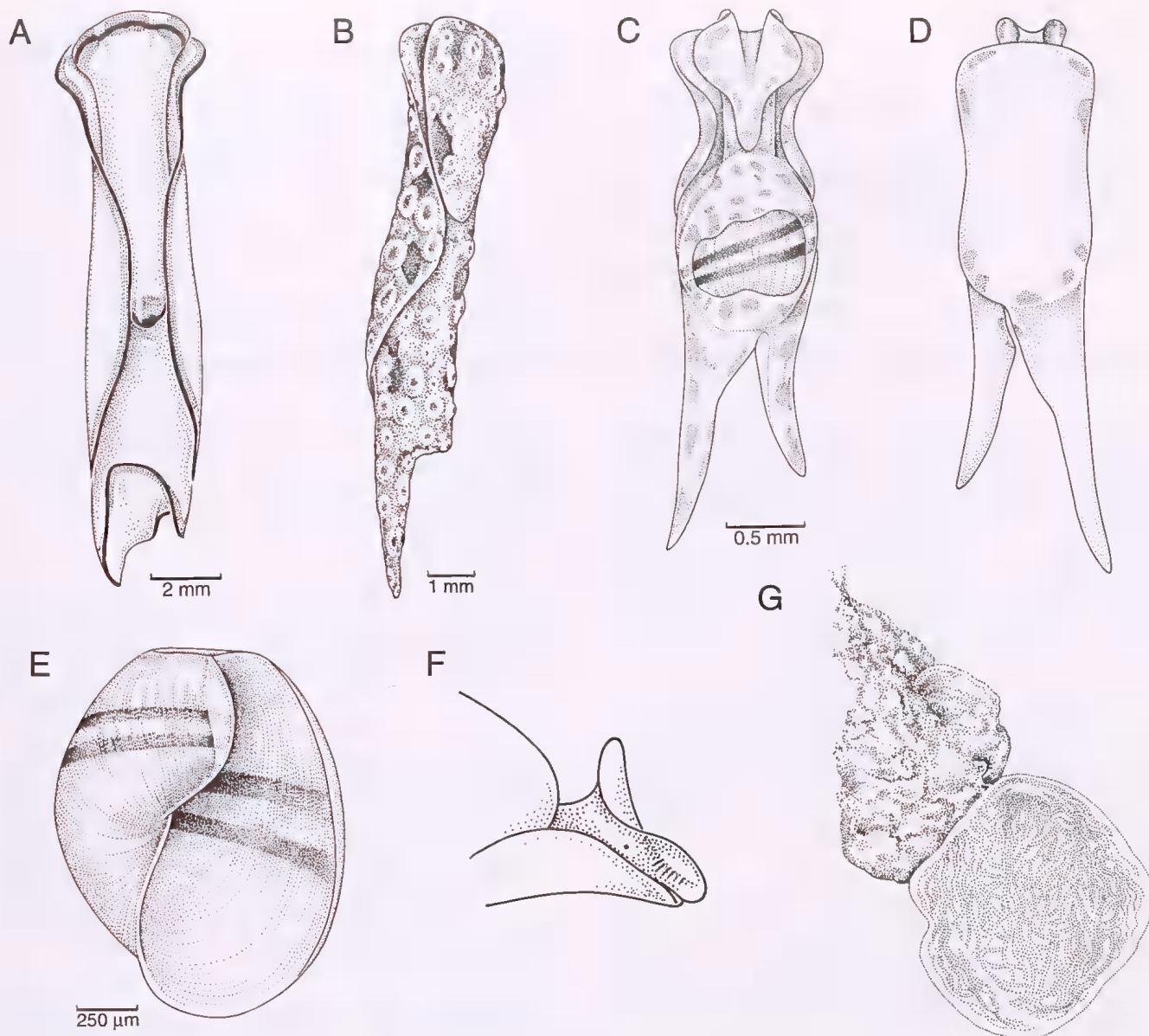


Figure 16.31 Family Aglajidae. A, *Chelidonura pallida*. B, *Odontoglossa guamensis*. C–F, *Noalda exigua*. G, *Philinopsis taronga*, egg mass. A, B, C, animal, dorsal view; D, animal, ventral view; E, shell, apertural view; F, head, lateral corner. (A, B, after photographs by I. Loch; C, D, F, after sketches by R. Burn; G, after photograph by F.V. Murray) [R. Plant]

rounded or conical papilla or linear flagellum. The visceral hump may have additional terminal protuberances. It is generally free of the foot posteriorly, but in a few species is confluent.

The foot is broad, rather longer than the visceral hump, and developed laterally into large, thin parapodia which meet dorsally or overlap over the visceral hump. A pedal gland is present in the posterior part of the sole. Hancock's organs are present in the lateral groove separating cephalic shield and foot, the penis opens on the right side behind the mouth, and an external seminal groove runs from the mantle cavity to the penial aperture. The mantle cavity is reduced, and hardly contains the small plicate gill, or is absent except for the dorsal ridge, when the gill hangs in the space between the visceral hump and right parapodium. In *Sagaminopteron*, the gill is large and well developed with long pinnules, and may project considerably above the visceral mass.

Gastropoterids generally have vivid specific colour patterns, as attested by the specific names *alboaurantium*, *citrinum*, *flavum*, *fuscum*, *nigromarginatum*, *ornatum*, *phychedelicum* and *rubrum*.

At the entrance to the pharynx, jaws composed of chitinous rods may be present or reduced, or are lacking. The radular row has a pair of large, curved lateral teeth, is generally denticulate along the inner edge, and has two to twelve smaller smooth marginal teeth. There is neither a median tooth, nor are there gastral plates. The circumoesophageal nerve ring is in front of the pharynx, the

cerebral ganglia are conjoined or separated by a short commissure, the intestinal ganglia are generally fused to the pleural ganglia, the visceral ganglion is either fused to, or a short distance from, the subintestinal ganglion, and the visceral loop is very short.

The invaginable penis generally has a papilla, and may have additional fleshy lobes or chitinous spines in the fundus of the sheath. The one or two prostate glands are generally short and simple, though elongate and convoluted in two species, and a sperm bulb, penial bulb and prostatic duct may be present. The function of all these parts during mating is little understood (Burn 1980). The female tract has a bursa copulatrix opening to the genital vestibule, and the seminal receptacle attached or forming part of the proximal spermoviduct. A few species have a small globular lobe attached to the lower posterior edge of each parapodium, but nothing is known of its function (Burn 1980).

Species of *Sagaminopteron* are invariably associated with particular species of the sponge genus *Dysidea* (Demospongiae) which is their probable food source. A minute bivalve and the remains of minute crustaceans have been found in the gut of other gastropoterids (Gosliner & Armes 1984; Gosliner 1989), but nothing is known of the food of the remainder of the family. Eggs are laid in a small gelatinous balloon anchored to the substratum by a mucous thread (Tokioka & Baba 1964; Carlson & Hoff 1973a; Gosliner 1989). In *Gastropoterion vespertilium*, veligers hatch 3–4 days after spawning (Gosliner & Armes 1984).

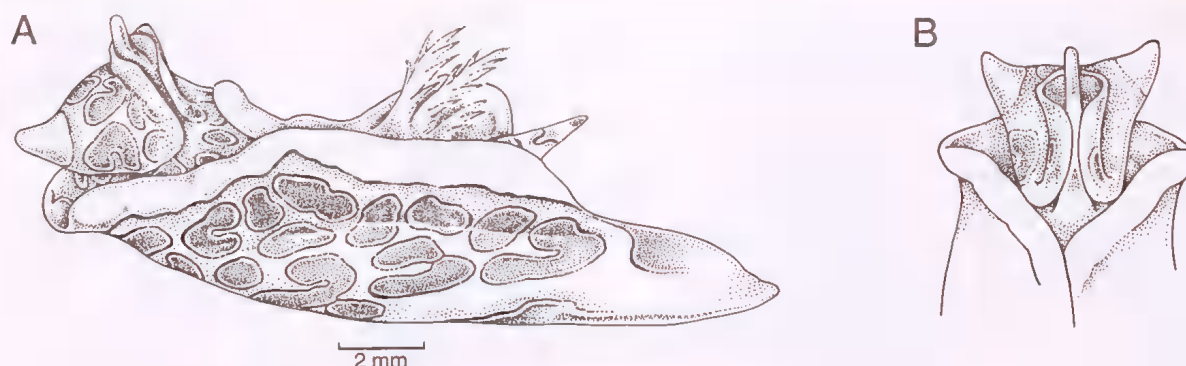


Figure 16.32 Family Gastropteridae. *Sagaminopteron psychedelicum*: A, animal, lateral view; B, head showing the cephalic shield and the posterior medial siphon, dorsal view. (A, B, after photographs by C. Carlson) [R. Plant]

The four genera in the family – *Gastropteron*, *Sagaminopteron*, *Siphopteron*, *Enotepteron* – are distinguished by differences in the siphonal and visceral hump formation, the gill, the radular teeth, and the male genital complex. The first three genera occur in Australian waters. *Gastropteron* occurs from intertidal waters to depths of 1500 m, and is represented by temperate and tropical species. The other genera are Indo-Pacific, ranging from South Africa to Hawaii, the Japan Sea to southern Australia. There is no fossil record, though the small, calcified haliotiform shell of *Sagaminopteron* should survive mineralisation.

The Indo-West Pacific *Sagaminopteron ornatum* (Pls 33.5, 33.6), bright pink in colour with yellow tips and margins, is the only species definitely recorded from Australia (Burn 1973a), with many records from the whole coastline. Other species have been reported from Queensland (Burn 1980), but the identifications have not been confirmed. Numerous species from Australian temperate and tropical waters await description or identification (R. Burn personal observation data).

The Gastropteridae have been well revised by Gosliner (1989). His earlier papers (Gosliner 1984, 1988), together with those of Tokioka & Baba (1964), Baba & Tokioka (1965) and Carlson & Hoff (1973a, 1974), should be consulted for taxonomic descriptions. Morphological aspects of *Gastropteron rubrum* have been dealt with by Vayssière (1880), Pelseneer (1894), and Guiart (1901), and those of *G. pacificum* by Bergh (1893b) and MacFarland (1966).

Superfamily HAMINOEOIDEA

An evolutionary progression is evident within this superfamily, from primitive forms with a heavy shell and large mantle cavity, to forms in which the shell is very reduced, the mantle cavity opens posteriorly and the body cavity becomes enlarged to accommodate the organs of the visceral spiral.

Rudman (1971a, 1972g) stated that the Haminoeidea has a reproductive system more like that of aplysiids than any other group of opisthobranchs, but not all authors agree (for example, Talavera, Murillo & Templado 1987). The posterior displacement of the circumoesophageal nerve ring from around the forepart of the buccal bulb to around the oesophagus behind the buccal bulb in some *Haminoea* species, with the marked shortening of the cerebral commissure in others and in smaragdinellids, suggests that haminoeoids are more advanced among the lower opisthobranchs than has been recognised previously.

Haminoeoids have in common a quadrate cephalic shield with slightly sinuate anterior edge, a pair of eyes which are usually visible through the dorsal integument and parapodia which arise from the foot margins to protect the neck and shell aperture. Hancock's organs are situated in the anterior part of the groove separating the cephalic shield from the foot. An operculum is present only during the veliger stage. Other features include a large plicate gill in the mantle cavity, an invaginable cephalic penis and external autospermal groove, a large muscular buccal bulb, and three transversely ribbed chitinous gizzard plates.

The herbivorous habit, the structure of the alimentary tract and the reproductive system indicate that *Phanerophthalmus* and *Smaragdinella* belong in the superfamily with *Haminoea*, *Bullacta* and *Atys* (Rudman 1972g).

Family Haminoeidae

The Haminoeidae have a greater diversity of shell shapes and abundance of species than any other living cephalaspidean family. The number of generic taxa, based mainly upon shell characteristics rather than valid anatomical differences, is exceeded only in the family Cylichnidae.

Haminoeoids (Fig. 16.33) are the only cephalaspideans to resorb or dissolve the inner whorls of the shell leaving only a tightly folded cord of periostracum (Marcus, Er. 1957, 1958b; Burn 1978). The largest haminoeid, the European *Haminoea navicula*, may attain a shell length of 32 mm, and, exceptionally, a body length of 70 mm (Thompson 1988). Shells of this size resemble thin, fragile, horn-coloured bullids. Most species, however, are much or very much smaller, the smallest having a shell length of 2–3 mm, and body about twice as long.

The shell is thin, fragile (except in *Atys naucum* and *Aliculastrum*) and transparent or translucent in life but opaque or horn-coloured when dried, occasionally (*Mnestia*, *Ventomnestia*) with stripes or bands of darker colour. It is usually smooth, with or without fine spiral striae, and with a very thin periostracum. The shape is broadly ovoid to narrowly cylindrical and always broadest at mid-length (Fig. 16.33B, C). The spire is always sunken, and often the posterior narrower part of the aperture extends beyond the spire with a thickened and twisted 'columellar' margin. The aperture is wider anteriorly, the columella is smooth without folds, and a thin columellar callus extends on to the last whorl. In the genera *Diniatys* and *Weinkauffia*, the columella is anteriorly truncate and forms a distinctive flange.

Anatomical and morphological knowledge of haminoeoids dates from Cuvier (1811), who discovered the transversely ribbed gizzard plates diagnostic of the superfamily. Living haminoeoids are similar in general appearance to bullids, but the shell is much less substantial. The cephalic shield is quadrate, and its anterior edge is slightly sinuate with the anterior corners folded down ventrally (Fig. 16.33A). The posterior margin is produced into a pair of rounded or elongate lobes, or more rarely a single, broad elongate lobe. The eyes are generally visible dorsally, often enclosed in small unpigmented areas.

The broad foot is shorter than the shell, and its lateral edges are raised up into parapodia to protect the neck and shell aperture. The parapodia often meet mid-dorsally above the animal. The infrapallial lobe (posterior mantle lobe, external posterior pallial lobe, epicochlear expansion) fills the shell aperture behind the foot, and may project beyond the shell as a tail or, exceptionally, as an extremely long flagellum with a papillate fleshy fold covering the posterior part of the shell (R. Burn personal observation).

The antero-lateral Hancock's organs are variously developed, ranging from a lightly cuticularised smooth patch, to an elongate, raised ridge along each side of the neck or an elaborately pinnate raised structure. A pair of small, smooth oral lobes flank the mouth. In the small infaunal species, *Cylichnatys campanula*, from southern Australia, the oral lobes have an elongate triangular area of minute crimson-coloured papillae (Burn 1978).

The body can generally retract fully within the shell. The mantle cavity opens to the right side and contains the large plicate gill. The invaginable cephalic penis may be unarmed, or armed with chitinous spines, and is continuous with the prostate gland. There may also be various accessory glands (Burn 1969; Rudman 1971a). An external seminal groove runs from the genital aperture within the mantle cavity to the penis. The bursa copulatrix, at the end of a long duct, opens into the genital vestibule. The smaller seminal receptacle is placed at the inner end of the spermiduct, often within the folds of the genital gland mass. Copulation is reciprocal.

Haminoeids are variably coloured, and some are able to change colour to suit the substratum (Edlinger 1982). Species crawling over mud-flats are sombre in colour, whereas infaunal and nocturnal species are pale cream to almost translucent, sometimes with small areas of darker pigment in the shell mantle. A few species of *Haminoea* are brightly coloured, often with orange, yellow, red or white spots and green or dark blue stripes on a greenish background (Pl. 33.4). The animal of a small *Micratys* from Lizard Island, northern Queensland, is bright and wholly red (R. Burn personal observation).

The buccal bulb is large and muscular. The jaws are composed of columnar chitinous rods, or polygonal bundles of rods, some of which project as denticles along one edge of the bundle. Each row of the radula has a small, often tricuspidate, central tooth, flanked on each side by one to 67 hook-shaped, or awl-shaped, lateral teeth. The innermost lateral teeth generally have minute to strong denticles along one side of the cusp. The gizzard contains three identical, brown chitinous plates, each longitudinally curved with a strong central outer rib, and transversely ribbed on the inner convex face. The ribs are incipient in some species and stronger and denticulate in others. The circumoesophageal nerve ring is situated in front of the buccal bulb (Rudman 1971a), or behind it (Guiart 1901; Marcus, Er. 1958b) as in smaragdinellids. The cerebropleural ganglia are concentrated, the subintestinal and visceral ganglia are close together, and the posterior end of the long visceral loop, with the supra-intestinal ganglion, is a long way back on the right side of the loop.

Details of spawning, ontogeny, anatomy, reproductive and nervous systems, and shells are to be found in the works of Pilsbry (1895), Vayssière (1880), Bergh (1901), Guiart (1901), Smallwood (1904), Habe (1952), Macnae (1962), Usaki (1966a, 1966b), Hurst (1967), Rudman (1971a, 1971b), Talavera *et al.* (1987) and Gibson & Fu-Shiang Chia (1989). The spawn of *Atys semistriata* is a globular mass 15 mm wide (Rudman 1971a), fixed to hard surfaces. The spawn of *Aliculastrum cylindricum* is eaten by a small indeterminate aeolid at Lizard Island (R. Burn personal observation). The Hawaiian *Haminoea crocata* is a preferred food of the molluscivorous *Conus pennaceus* (Kay 1979).

Haminoeids are herbivorous, grazing on turfing green algae such as *Enteromorpha* (Rudman 1971b), rather than carnivorous and feeding on bivalves as claimed by Macpherson & Gabriel (1962). Many species of *Haminoea* (Pl. 33.4) and *Liloea* (Fig. 16.33A) crawl about on reefs and mud and sand flats at low tide. *Atys semistriata* rests infaunally during the day, and emerges at night to feed. Haminoeids mostly occur in shallow waters, to depths where sunlight penetrates. They are plentiful in tropical and temperate seas, and are known from all parts of the Australian coastline. Some of the smaller species have been reviewed by Burn (1978), and Short & Potter (1987) figure a few large Queensland species.

There are two primary genera in the family, *Haminoea* and *Atys*. Both have been unnecessarily subdivided on shell characters alone into many genera, subgenera and sections (Vaught 1989), the limits

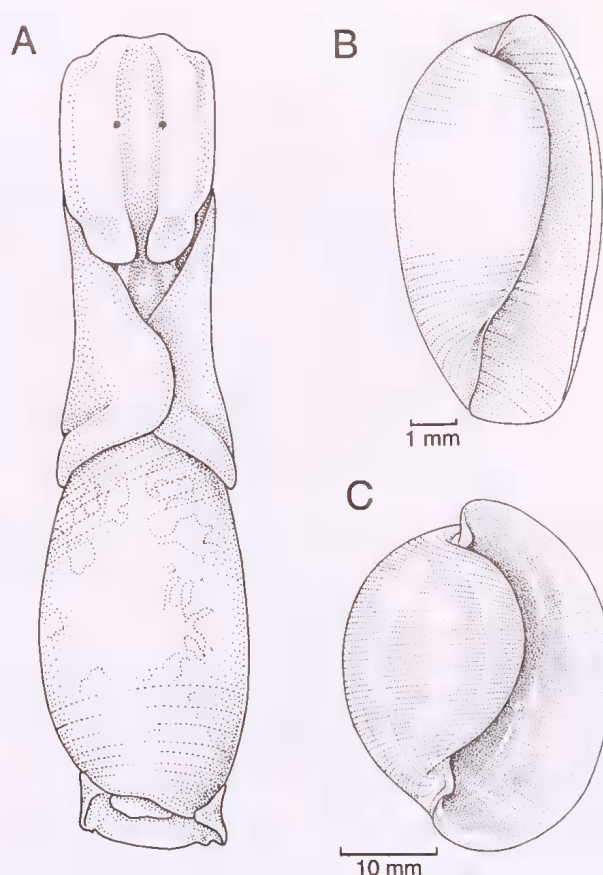


Figure 16.33 Family Haminoeidae. A, B, *Liloea* sp. C, *Atys haucum*. A, animal, dorsal view; B, C, shell, apertural view. (A, after sketch by R. Burn)

of which are poorly understood. At present, it seems reasonable to include the following taxa in the family (those marked * are not reported from Australia): *Haminoea*, *Liloea*, *Haminella**, *Atys*, *Aliculastrum*, *Limulatys*, *Nipponatys*, *Mimatys**, *Micratys*, *Cylichnatys*, *Roxaniella**, *Weinkauffia**, *Austrocyllichna*, *Diniatys*, *Mnestia*, *Ventomnestia*. Haminoeids first appear in the fossil record of the Palaeocene (Zilch 1959–1960). At least one species of *Atys* occurs in the Early to Middle Tertiary beds of Victoria (R. Burn personal observation), and *Liloea brevis* occurs in the early Pleistocene Quaternary beds of South Australian and southern Western Australia (Ludbrook 1978, 1984).

Family Bullactidae

The Bullactidae are a monotypic family presently known only from the great estuaries of the Chinese coastline. The shell is philinid in shape with a small last whorl and greatly expanded aperture (Fig. 16.34). It is fragile, finely sculptured, and has a thin periostracum.

The animal was described by Bergh (1901), Annandale (1924), and Tchang-Si (1934). The radular row has a small plate-like, possibly caducous, central tooth, flanked each side by a large hooked lateral tooth, and, some distance away, 12 smaller hooked marginal teeth. The gizzard contains three narrowly triangular chitinous plates with strong, chevron-shaped transverse ribs. The penis has a strong apical stylet to the large papilla, a complex prostate gland, and a long accessory prostate gland.

Family Smaragdinellidae

Members of the genera *Smaragdinella* and *Phanerophthalmus*, with about eight species, comprise the Smaragdinellidae (Fig. 16.35). At least one species of each genus occurs along Australia's tropical northern coastline. Rudman reviewed (1972g) most aspects of the morphological and evolutionary trends within the family. The solid shell of *Smaragdinella* is mostly external,

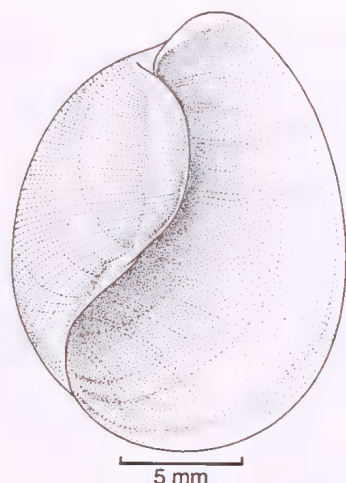


Figure 16.34 Family Bullactidae. *Bullacta exarata* shell, apertural view. [R. Plant]

oval and flattened, and lacks the upper whorls except for a small cup-shaped projection (Fig. 16.35C). In *Phanerophthalmus*, the shell is more reduced and wholly or almost wholly internal. It is shaped like a shallow quadrate plate with one thickened edge (the remnant of the columella) and drawn out into a point on the posterior margin of the apertural lip.

The body form of *Smaragdinella* species resembles a small, thickened gelatinous *Hamineoidea* species, with a single broad posterior lobe of the cephalic shield, and high, thick parapodia held mostly over the shell (Fig. 16.35A). It lives in exposed intertidal situations on rocky shorelines and nestles into small damp holes and crevices (Miller 1969) or around barnacles and rock oysters (Habe 1964).

The elongate cylindrical body of *Phanerophthalmus* species (Fig. 16.35B) resembles that of aglajid opisthobranchs or elysioid sacoglossans. The cephalic shield is drawn out posteriorly into two small lobes, and the long foot has large lateral parapodia folded over the dorsum. These animals live in and near seagrass beds and reef areas (Rudman 1972g).

In both genera, the Hancock's organs are slightly ridged, the radula is broad with a small, tricuspidate central tooth and 15 to 37 smooth lateral teeth each side, the gastral plates have numerous small V-shaped ridges, and the circumoesophageal nerve ring is behind the buccal mass. A long duct links the penis to the spermathecal bulb in *Phanerophthalmus*, either free or through a muscular swelling. *Smaragdinella* species have accessory and prostate glands as well as a spermathecal bulb.

Despite good descriptions of mostly preserved material (Eales 1938; Marcus, Er. & Burch 1965; Marcus, Ev. & Marcus, Er. 1969a; Rudman 1972g), little ecological information is available on smaragdinellids (Habe 1964; Miller 1969; Rudman 1972g; Kay 1979; Gosliner 1987a).

Family Incertae sedis

The rare genus *Hamineobulla* is also considered to be haminoeoid (Kitao & Habe 1982). The only Australian record is of a single broken specimen, with animal, of the type species, from 77 m off Cape Moreton (R. Burn personal observation). The thin shell has a typical ovoid *Hamineoidea* shape, with fine spiral sculpture (Habe 1950b, 1964). The cephalic shield has a pair of posterior lobes, and the eyes are visible through the dorsal surface. The Hancock's organs have low ribs. Jaws are present just within the mouth. The radular row has no central tooth, only a pair of smooth, hooked laterals. The gizzard has three chitinous plates, all of the same shape but laterally compressed in various ways, each basically with a single V-shaped ridge on the face. The penis has both accessory gland and spermathecal bulb (R. Burn personal observation).

The available data suggest that *Hamineobulla* could belong to the Haminoeidea, but its affinities and status are far from settled.

The well-known but little studied genus *Roxania* (= *Abderospira*, *Damoniella*) has been variously classified with cylichnids (Thiele 1931; Platts 1985; Thompson 1988) and haminoeids (Bouchet 1975; Høisæter 1986; Gosliner 1987a). The animal has long posterior lobes on the cephalic shield, and the eyes do not show through the dorsal integument (Forbes & Hanley 1848–1853). The foot is short, the infrapallial lobe is expanded laterally into an incomplete mantle almost covering the shell. The external shell is ovoid, solid, and spirally punctate, the internal whorls are retained, and there is a thin periostracum. The nerve collar encircles the front part of the buccal bulb, the penis has both a prostate gland and a seminal bulb, and there is an external seminal groove (R. Burn personal observation). The radular row has a broad central tooth with a number of large and small denticles, and each side a quadrate lateral tooth with one or more denticles along one edge. Most reports indicate that there are no gizzard plates, but Gantes & Cornet (1981) found three small fragile chitinous plates, not unlike those of *Hamineobulla* (Kitao & Habe 1982).

Roxania is a benthic genus, living to a depth of 1500 m. Its fossil history dates from the Cretaceous of Europe (Zilch 1959–1960). In Australia, there are several Middle Miocene and Pliocene species (Ludbrook 1958). Recent species have been described from the Indian Ocean (Thiele 1925) and the northern Pacific (Habe 1964), but as yet the genus is unknown in Australian waters. The deep water *Leucophysema* is probably closely related to *Roxania*. The systematic position of *Roxania* remains unresolved.

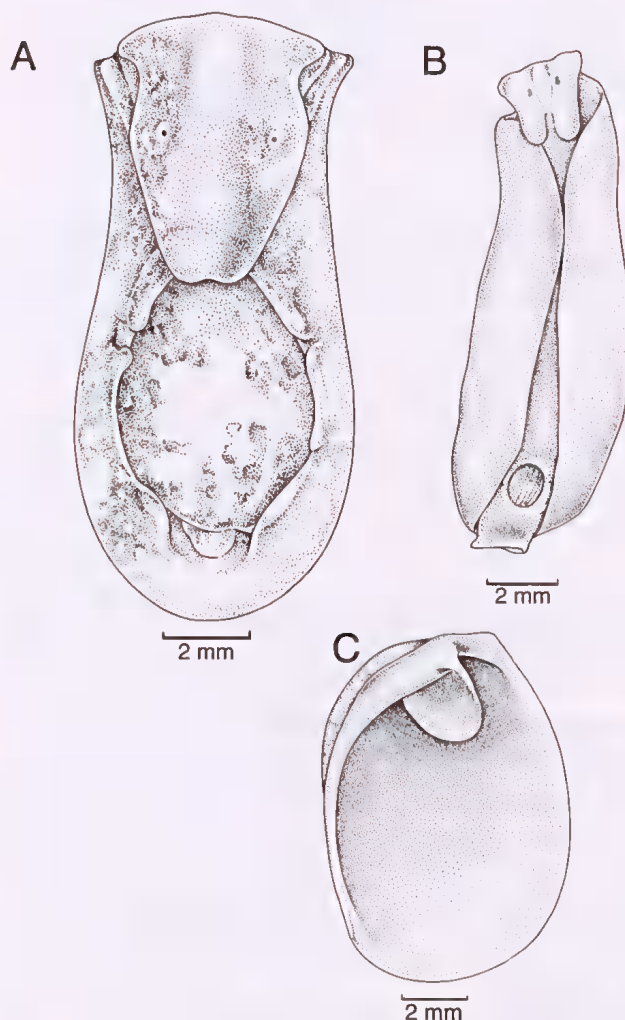


Figure 16.35 Family Smaragdinellidae. A, *Smaragdinella calyculata*. B, *Phanerophthalmus smaragdinus*. C, *Smaragdinella viridis*. A, B, animal, dorsal view; C, shell, apertural view. (A, B, after sketches by R. Burn) [R. Plant]

Superfamily BULLOIDEA

The herbivorous bulloideans are represented worldwide by one family and relatively few species. The large, ovoid and solid shell can contain the animal, and there is no operculum. Small parapodia are present at the side of the foot. The distinctive radula is unlike that of any other cephalaspidean. A broad, denticulate rachidian tooth is flanked by two smaller, cuspidate lateral teeth and a much smaller polygonal plate. The inner lateral is denticulate along both edges of the cusp, the other along the marginal edge. The gizzard contains three uniquely shaped, almost identical plates, with chitinous accessory spines between the ends of the plates.

The pre-pharyngeal nerve ring is concentrated, but the lateral connectives between the cerebral and pleural ganglia are still distinct. The visceral loop is long and slightly twisted posteriorly. The supra-intestinal ganglion lies above the level of the subintestinal ganglion, and is closer to the visceral ganglion than to the nerve ring. The supra-intestinal and visceral ganglia are as large as the ganglia of the nerve ring, and the latter is partly fused with the small subintestinal ganglion at the end of the visceral loop.

Bulloideans are usually grouped with haminoeoidae. However, bulloideans may be separated effectively on the basis of having a larger and thicker shell in which the embryonic and inner whorls are retained, a broad rachidian tooth in the radula, uniquely shaped gizzard plates, and an oesophageal diverticulum.

Family Bullidae

The family Bullidae includes the largest of the shell-bearing cephalaspideans (Fig 16.36). The ovoid external shell is up to 67 mm long (Ludbrook 1978), robustly calcified, very smooth and greatly inflated, and has a deeply sunken or involute spire. The aperture is at least as long as the shell, broadly rounded anteriorly and more restricted posteriorly. The columella lacks ridges or folds, but a conspicuous, thin columellar callus is present. The shell is mottled or spotted in drab colours, often with one or two darker bands. The narrower shell seen in the juvenile and its slender aperture which extends well beyond the truncate spire, have led to confusion with unrelated genera (Thompson *et al.* 1985).

The body is dull yellow to dark orange, with or without lighter flecks. The cephalic shield is produced antero-laterally so as to form a pair of inrolled or siphon-like tentacles, and posteriorly into a pair of broadly triangular lobes covering the anterior part of the shell (Fig. 16.36). The eyes lie close to the dorsal surface of the cephalic shield and are conspicuous. The foot is large and longer than the shell, with small parapodia which are folded up laterally to

protect the neck region of the body and the aperture of the shell. The animal can retract completely into the shell. An operculum is present in the veliger stage only (Farfan & Ramirez 1988).

The siphon-like tentacles of the cephalic shield draw water over the chemosensory Hancock's organs. These lie in the anterior part of the groove separating the cephalic shield from the foot. On the right side, the water is channelled backwards through the tunnel formed by the parapodial fold to enter the mantle cavity (Rudman 1971b). The mantle cavity opens externally on the right side and contains a large plicate gill. The unarmed penis is invaginable, and continuous with a long much-coiled prostate gland. There is an external seminal (autospermal) groove. A very small seminal receptacle (spermatocyst) is present and may be contained within the walls of the common genital duct adjacent to the duct to the bursa copulatrix (spermatheca). The animal produces copious amounts of viscous mucus as it moves through the surface of the substratum, and eventually forms mucous tunnels marking its path (Paine 1963).

The buccal bulb is large and muscular. Just within the mouth is a pair of jaw plates composed of closely packed columnar chitinous rods (Marcus, Er. 1957; Rudman 1971b). Each row of the radula comprises five teeth between a pair of small, irregular quadrate marginal plates (formula 1.2.1.2.1). The broad, short, central tooth, with 10 or more denticles, is flanked on each side by an inner symmetrical and an outer asymmetrical denticulate lateral tooth. The midgut or gizzard encloses three large identically shaped, strongly keeled and ridged, brown chitinous grinding plates with a band of chitinous spines before and behind. The circumoesophageal nerve ring encircles the anterior part of the buccal mass, the cerebral commissure is long and thick, and the visceral loop is long (Eales 1938; Marcus, Er. 1957).

Aspects of spawning, ontogeny and anatomy, including that of the reproductive and nervous systems have been described by Er. Marcus (1957), Rudman (1972g), Robles (1975), and Farfan & Ramirez (1988). The spawn of *Bulla quoyii* is a flaccid balloon of red eggs, some 20–30 mm long, fixed by one end to the substratum (Willan & Morton 1984). Copulation (probably reciprocal) and oviposition have been observed at night (Marcus, Er. 1957; Robles 1975).

Bullids are predominantly nocturnal animals, which emerge to feed on epibenthic algae during the hours of darkness and rest infaunally during the day (Rudman 1971b; Robles 1975). They are shallow water animals, often in estuarine or lagoonal embayments, and prefer areas of soft sandy mud. Mass mortality has been reported following freshwater flooding of mud flats (Stebbins 1987). Claims that *Bulla* feeds on molluscs which are swallowed whole and crushed by the gizzard plates (Macnae 1962; Coleman 1975) are unsubstantiated. Predators on *Bulla* species include the giant aglajid *Navanax* (Paine 1963) and fish (Burn 1966a).

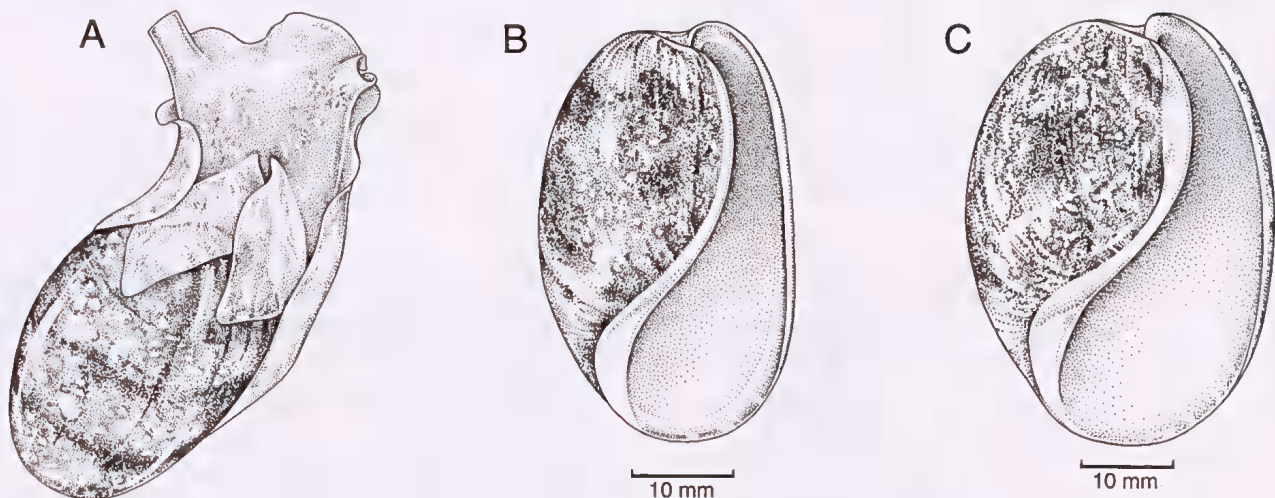


Figure 16.36 Family Bullidae. A, B, *Bulla quoyii*. C, *Bulla ampulla*. A, animal, dorsal view; B, C, shell, apertural view. (A, after photograph by J.H. Black) [R. Plant]

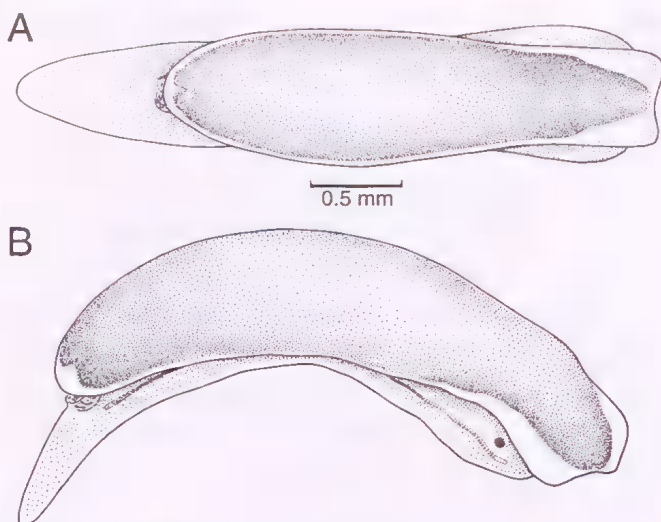


Figure 16.37 Family Runcinidae. *Runcina australis*, animal: A, dorsal view; B, right dorso-lateral view. (A, B, after sketches by R. Burn) [R. Plant]

Despite an array of generic and specific names, the family Bullidae is monotypic, with relatively few species in the genus *Bulla*. The background to some of the nomenclatural complexity was described by Willan (1978a). Three large, widespread Indo-Pacific species (*B. ampulla*, *B. vernicosa* and *B. punctulata*) are common along Australia's tropical northern coastline, and a smaller fourth species (*B. angasi*), known from the south-western Pacific including central and northern New South Wales and northern New Zealand, is much less common (Short & Potter 1987). The common southern Australian and New Zealand species is *B. quoyii* (= *B. botanica* of Australian literature and collectors) (Fig. 16.36A; Wells & Bryce 1986). *Bulla* has a long palaeontological history, dating from the Upper Jurassic of Europe (Zilch 1959–1960). In Australia it appears in the Early Pleistocene and Quaternary beds of South Australia and southern Western Australia (Ludbrook 1978, 1984).

Superfamily RUNCINOIDEA

Runcinoideans are small, highly specialised opisthobranchs. The undivided notum, the complete lack of a mantle cavity, and the four gizzard plates readily separate them from other cephalaspideans; their other attributes are also found among the less specialised superfamilies.

Runcinoideans are found in shallow seas down to a depth of 50 m. They have a slug-like body less than 9 mm long and are somewhat flattened dorso-ventrally. The cephalic shield and visceral mass are confluent dorsally, with no trace of any transverse division, and the notum overhangs the subpallial groove all around. Tentacular projections, parapodia and caudal expansions of the foot are all lacking. A minute reduced shell may be present at the posterior end of the notum; it can be external or internal. Eyes are generally prominent dorsally, and Hancock's organs are present on each side in the anterior subpallial groove. The jaws and radula are well developed, and the gizzard generally contains four identical chitinous triturating plates.

The circumoesophageal nerve ring is positioned behind the pharynx, the intestinal ganglia about the cerebropleural ganglia, the visceral ganglion is fused to the subintestinal ganglion, and the visceral loop is very short. The gill is posterior right lateral, or terminal, or lacking. The anus is terminal, opening just to the right of the mid-line, and the renal and genital apertures are close by on the right side. A pallial or opaline gland opens below or to the left of the anus. The external seminal groove runs along the right body wall, leading to the invaginable cephalic penis. Some species produce spermatophores, and some pass through an encapsulated embryonic development with few typical veliger phases. An operculum is lacking, even in the embryonic stages.

The classification proposed by Burn (1963a) is no longer satisfactory, because of the subsequent proliferation of both generic and specific taxa. Worldwide, eight generic and 29 specific taxa are in use, with more species recorded from the Mediterranean and European coastlines than elsewhere. There are two families, each represented in Australian waters by a single described species.

Family Runcinidae

Typical runcinids have a posterior gill and four transversely ribbed gizzard plates. The gill usually comprises a single plicate plume, but there may be two or three arising separately from the body wall to the right of the anus. More rarely, the gill is a circlet of small separate tufts around the anus (*Runcinella*), or a band of tufts dorsal to, or each side of, the anus (*Runcinida*). The reduced shell may be cup-like and external (*Lapinura*), plate-like and external (*Ildica*), or internal, vestigial or lacking (*Metaruncina*, *Runcina*, *Runcinella*, *Runcinida*). The body is smooth and slender and the tail is longer than the notum (Fig. 16.37). The notal margin above the Hancock's organs is often flexed upwards to form shallow inhalant siphons.

The male copulatory organ comprises spermatid bulb, prostate gland, penis and penial sheath. Sperm transfer in *Runcina* and *Metaruncina* is by ovoid or pyriform spermatophores (Ghiselin 1963; Baba 1967; Kress 1985a). The bursa copulatrix may be attached by a long duct to the genital vestibule (Miller & Rudman 1968; Gosliner 1991), or a modified, highly ciliated portion of the lower spermoviduct may act in this capacity (Baba 1967; Marcus, Er. & Marcus, Ev. 1970; Kress 1977).

The jaws are strong and composed of sharp, pointed chitinous rods. The radular row comprises an arched or bilobed central tooth, and one or two large hooked lateral teeth on each side. The teeth may be smooth or denticulate. *Metaruncina* has a degenerate radula in which the teeth are all deformed and clumped together (Baba 1954). The transverse ribs on the gizzard plates are generally irregular and may bear denticle-like points. The post-gizzard oesophagus may contain additional cuticularised conical teeth.

Runcinids lay small egg masses containing 20 to 100 eggs of 250–350 μm diameter. Small crawling juveniles emerge some 38–42 days later (Baba & Hamatani 1959; Thompson 1976). *Runcina* dies after a single spawning season (Kress 1985a). Details of runcinid functional and comparative anatomy are given by Vayssière (1883), Odhner (1924), Ghiselin (1963), Miller & Rudman (1968), Er. Marcus & Ev. Marcus (1970), Rudman (1971b) and Kress (1985a, 1985b), and of the embryonic (direct) development by Baba & Hamatani (1959).

Most runcinids are small, dark, worm-like animals. Their colour ranges from black through brown and red to green and they may have paler or darker lateral areas, longitudinal stripes, or transverse bands. Some species are highly coloured. The sage green body of *Runcinella zelandica* is marked by bright salmon stripes and zigzags along the notum (Willan 1981a). *Runcina fijiensis* is pale yellow with black longitudinal stripes along both notum and tail.

Runcina australis (Fig. 16.37) is the only runcinid species currently recorded from Australian waters (Burn 1963a). It is greenish-black in colour with lighter lateral areas on the head. At times it is quite common intertidally and subtidally among coralline algae fringing rock pools and reefs, or among the seagrass *Amphibolis antarcticus*. It ranges from central New South Wales through Victoria to south eastern South Australia. Additional species including *R. fijiensis* are known (but not yet recorded) from both temperate and tropical coastlines (R.C. Willan personal communication; R. Burn personal observation). Further species are found throughout the western Pacific region, with two each from New Zealand, Fiji and Japan.

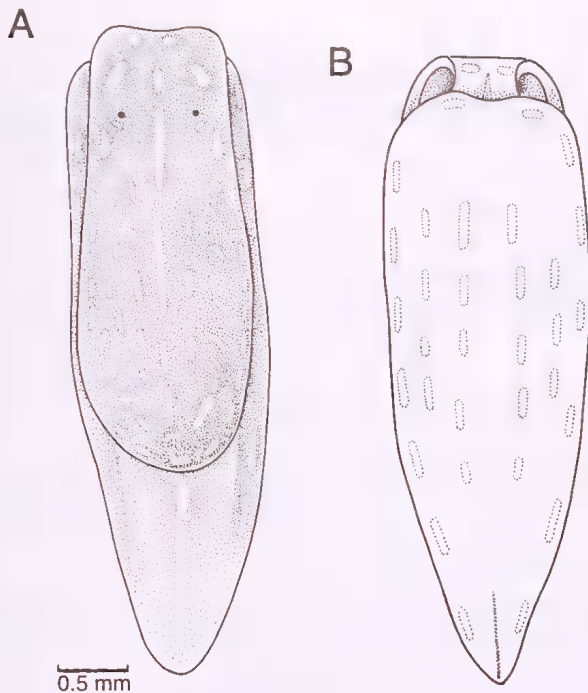


Figure 16.38 Family Ilbiidae. *Ilbia ilbi*, animal: A, dorsal view; B, ventral view. (A, B, after sketches by R. Burn) [R. Plant]

Family Ilbiidae

Three western Pacific species are referred to this poorly known family. Ilbiids have no shell, no gill and no gastral plates, but otherwise resemble runcinids very closely (Fig. 16.38). The jaws are large and the elements denticulate. The radular row of *Ilbia* has a large tricuspidate central tooth and a bicuspidate denticulate lateral tooth on each side. In *Pseudoilbia*, there are four cuspidate and denticulate teeth; the two inner teeth (one large, one small) may represent the remains of a large central tooth, and the two outer teeth are broader versions of the lateral teeth of *Ilbia*. The penis has a sperm bulb, and the bursa copulatrix is attached to the genital vestibule. The foot may have a posterior pedal furrow. Nothing is known of food preferences or embryology.

Ilbiids have brightly coloured bodies. *Ilbia ilbi* is purple-mauve with yellow stripes (Burn 1963a). *Pseudoilbia lineata* has a white patch at each end of the notum with five bands of mottled black between (Miller & Rudman 1968), and *P. mariana* is white with yellow spots and dark brown patches (Hoff & Carlson 1990).

Ilbia ilbi is known from only a few collections from north-central New South Wales to western Victoria, where it has been found crawling on algae in reef pools. *Pseudoilbia lineata* has been found only once, on coralline algae in a pool in northern New Zealand, and *P. mariana* is widespread in the Marianas, where it occurs on algae on the reef flat down to 14 m.

Superfamily INCERTAE SEDIS

Family Notodiaphanidae

The little known family Notodiaphanidae, of uncertain affinity, is based upon a single species, *Notodiaphana fragilis*, (Vélain 1877) from St Paul Island in the southern Indian Ocean. Disparities between the only two figures of the shell (Fig. 16.39A, B) suggest that two species, if not genera, are involved. The species studied by Boss (1982) has a small, *Haminoea*-like, external shell, which is fragile, colourless and spirally striate, and a foot without parapodial lobes. The radular row has a quadrate lateral tooth with three cusps, and two subquadrate marginal teeth each with one cusp (Fig. 16.39C); the central tooth is lacking, as are gizzard plates. The circumoesophageal nerve ring lies in front of the pharynx, and an open seminal groove is present. The original material was found under stones at low water (Vélain 1877).

If the 'lateral' teeth of the radula examined by Thiele were, in reality, a fractured central tooth, *Notodiaphana* closely resembles the problematic haminoeoid genus *Roxania*.

Order ACOCHLIDEA

The Acochlidoidea is the least well-understood order of opisthobranch molluscs. It contains members which dwell in the interstices of gravel, sand and mud. Most are marine, although a few larger species live in freshwater streams, presumably feeding upon the micro-organisms which inhabit that environment. Acochlidoidea are generally small and have probably been derived from some group of primitive cephalaspideans, perhaps resembling the modern Diaphanidae.

Neither a shell nor an operculum is present in the adult phase. Calcareous spicules may be present in the skin. The body is small, usually less than 10 mm in length, except in the freshwater acochlidiids which can reach 35 mm. The cephalic shield is fused with the dorsal mantle, and may bear oral tentacles or antero-dorsal rhinophoral tentacles, or both. The elongate foot has a free, tapering tail at the rear. The visceral mass projects as a dorsal sac from the body, usually hiding the tail. There is neither mantle cavity or gill, nor, internally, jaws or gizzard plates. The radula is narrow, sometimes with only a single tooth on each side of the rachidian in each row. Obsolete teeth are discarded, not retained in a special sac. The sexes may be separate or united (hermaphroditic). The penis, if present, may or may not be armed. The central nervous system is euthyneurous, forming a ganglionic ring in front of the buccal bulb.

In the most recent revision (Arnaud *et al.* 1986), Acochlidae is treated as a suborder, divided into two superfamilies and five families. An earlier, well-documented classification (Rankin 1979), which treated them as one order, with five suborders, two superfamilies and 13 families for the 25 known species, is not presently accepted.

This order is known mainly from a few marine localities in the Northern Hemisphere and its importance in Australian ecosystems is yet to be determined. There are at present no published records of Australian species, but at least two species occur on the sandy beaches of Lizard Island, Queensland (R. Burn personal observation). Other species have been reported from the islands to the north and east of Australia: the composition of the interstitial fauna and the ecology of the interstitial opisthobranchs from the Solomon Islands have been studied by Challis (1969c, 1969d, 1970).

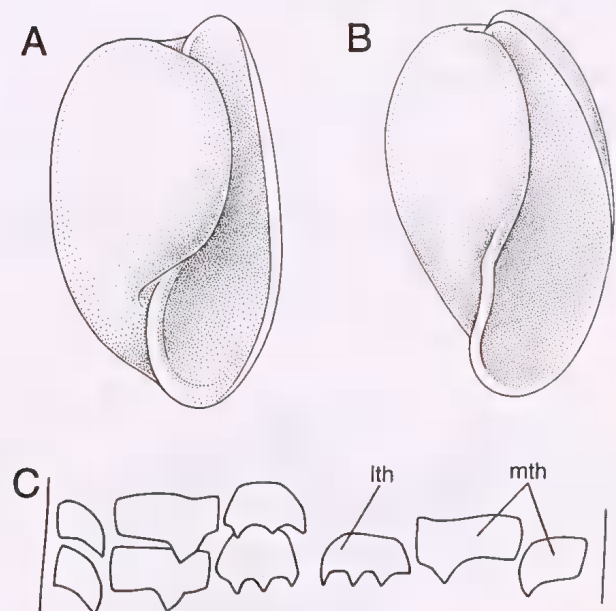


Figure 16.39 Family Notodiaphanidae. *Notodiaphana* spp.: A, B, shells, apertural view; C, radula, a transverse tooth row, the central tooth is lacking. lth, lateral tooth; mth, marginal teeth. (A, C, after Thiele 1912; B, after Vélain 1877) [R. Plant]

Superfamily ACOCHLIDIOIDEA

This superfamily contains species with a well-developed seminal groove or vas deferens, an armed penis, spermatozoa with a pyriform stoutish spiral head, few accessory ganglia associated with the anterior cerebral nerves, and a distinct foot. The radular row has a large denticulate central tooth flanked on each side by a lateral plate; there may be a second, smaller, plate on one side.

Family Acochliidiidae

Members of the type genus *Acochlidium* of the freshwater family, Acochliidiidae, are relatively large (up to 35 mm long) (Fig. 16.40) and hermaphroditic. The visceral sac is broad and leaf-like, and may have a wavy, glandular, posterior lateral margin. There are one or two pairs of head tentacles, and the eyes are visible dorsally. These animals are found under stones in flowing water. Species have been described from the Indonesian islands of Ambon, Flores and Sumba, and from Palau (Wawra 1980) and Fiji (Haynes & Kenchington 1991). There is also ■ record from the north-west coast of Irian Jaya near Sorong (D. McMichael personal communication). Suitable stream habitats may occur in northern Queensland.

Family Hedylopsidae

This family includes the large (up to 30 mm long), limnic genus *Strubellia*, and the much smaller (up to 5.5 mm long), marine genus *Hedylopsis* (Fig. 16.41). The head bears flattened or cylindrical oral tentacles, and a pair of smooth rhinophores. The eyes are visible dorsally. The visceral sac is cylindrical or elongate conical. *Strubellia* is dioecious; *Hedylopsis* species are sequential hermaphrodites, their sperm thought to be transferred by hypodermic injection of the penial stylet to any part of the body (Wawra 1989). *Strubellia* species occur in streams on Ambon, Indonesia, and in the Solomon Islands (Wawra 1974, 1988). No *Hedylopsis* have been found in the Australasian region.

Superfamily MICROHEDYLOIDEA

The three families grouped here are components of the marine interstitial fauna. All are characterised by sperm transfer in spermatophores, the lack of a penis, sperm with a long corkscrew-like head, and numerous accessory ganglia associated with the anterior cerebral nerves. The foot, eyes and rhinophores tend to be reduced. The visceral sac is cylindrical or sausage-shaped. All animals can partly or wholly retract the head-foot into the anterior part of the visceral sac.

Family Asperspinidae

In asperspinids, a dense layer of rod-like spicules in the visceral sac forms a pseudo-shell or a roof-like subepidermal cover (Arnaud *et al.* 1986). The head has two pairs of tentacles, eyes are absent, and the radula has up to two lateral teeth on each side of the denticulate rachidian. The reproductive system is hermaphroditic. Asperspinids (Fig. 16.42A), are small, ranging from 1–3 mm in length, and most species are from the North Atlantic.

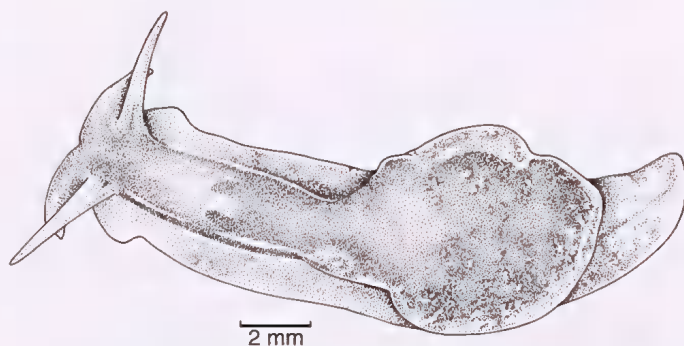


Figure 16.40 Family Acochliidiidae. *Acochlidium fijiense*, dorsal view. (After Haynes & Kenchington 1991) [R. Plant]

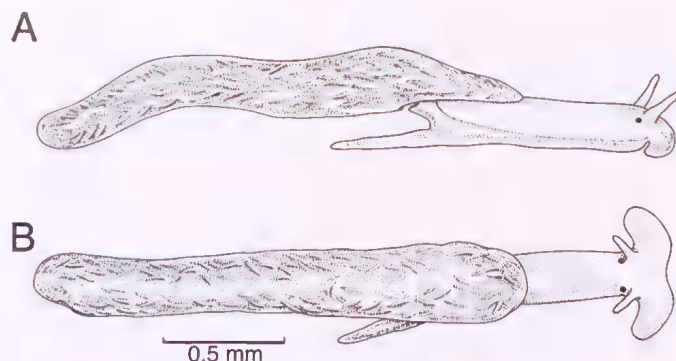


Figure 16.41 Family Hedylopsidae. *Hedylopsis suecica*: A, lateral view; B, dorsal view. (After Arnaud, Poizat & Salvini-Plawen 1986) [R. Plant]

Family Microhedylidae

The members of this family have minute, ring-shaped or plate-like spicular elements, allowing the body to contract and twist and turn very easily. The radula is similar to those of the Asperspinidae. The head has either two pairs of tentacles, or only oral lobes. The sexes are separate. These animals are 1.5–7.5 mm in length. Two species, now both doubtfully referred to *Microhedyle*, have been described from the Solomon Islands (Challis 1970).

A relatively large form found at Lizard Island (R. Burn personal observation) closely resembles *M. cornuta* (Fig. 16.42B) from the Solomon Islands but, at 10 mm, is three times larger.

Family Ganatidae

The family Ganatidae comprises two monotypic genera *Ganitus* and *Paraganitus*, grouped on the basis of having a pair of cuticular jaws, a monoserial radula of somewhat sacoglossan-like teeth, reduced rhinophores, and separate sexes. The animals range from 1.8–2.2 mm in length. *Paraganitus ellynnae* (Fig. 16.42C) has been recorded from the Solomon Islands and Vanuatu (Challis 1968).

A relatively small form found at Lizard Island (R. Burn personal observation) is identified tentatively as *P. ellynnae*.

Order RHODOPEMORPHA

Rhodopemorphs are small interstitial and epiphytic animals 'of uncertain systematic rank and affinity', regarded as a 'specialised off-shoot from the lower opisthobranchs' (Salvini-Plawen 1991). Support for this view comes from studies of the circumoesophageal nerve ring of two species by Haszprunar & Huber (1990).

The animals are turbellarian-like (Fig. 16.43), and lack a delimited head and foot, as well as tentacles, radula, jaws and heart. The shape of spicules in the epidermis is species specific, and a patch of adhesive glands is present at the posterior tip of the sole. The animals grow to 8 mm in length but are usually less than half this size. Some species have red pigment on parts of the body. The eyes are deep within the body, and the anus and single genital aperture open on the right dorso-lateral area between the first and third quarter of the body length. The anterior part of the body can retract ■ short way into the body. The circumoesophageal nerve ring encircles the oesophagus behind the foregut, and the very short visceral loop has only one ganglion, the visceral. The chromosome number is $n = 16$, $2n = 32$.

The order comprises one family, Rhodopidae, two genera *Rhodope* and *Helminthope*, and six species. The best-known species, *Rhodope veranyi*, lives in the Adriatic Sea and adjacent Mediterranean seas where it inhabits calm subtidal waters with stones and *Ulva* and feeds upon the larvae of the sponge *Trichoplax*. It lays groups of six to 30 eggs which develop directly

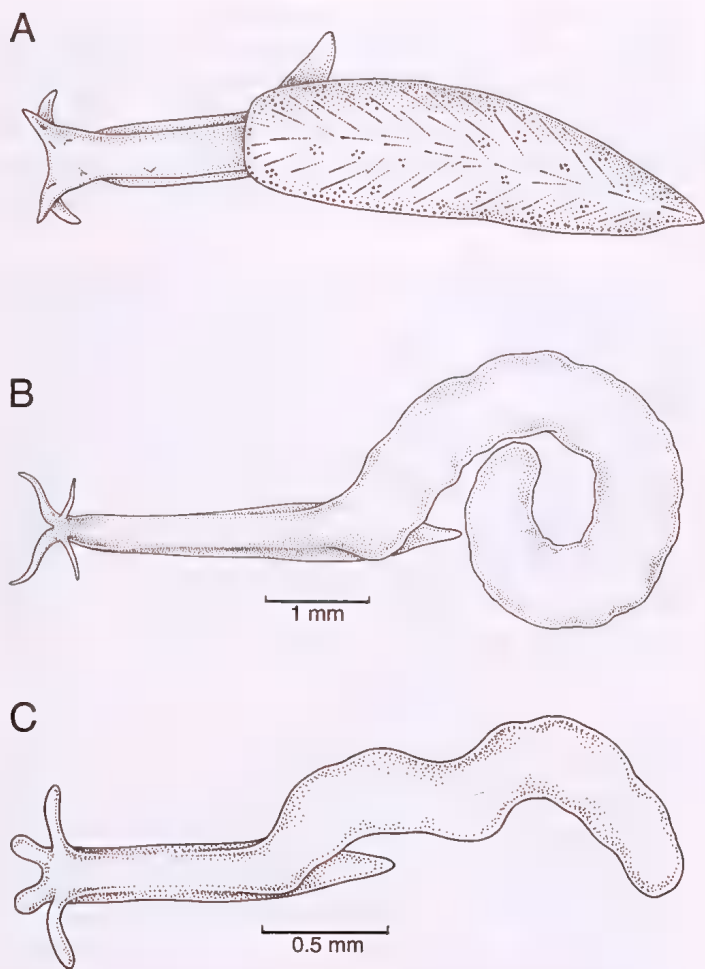


Figure 16.42 Superfamily Microhedyoidea. A, family Asperspinidae, *Asperspina brambelli*, dorsal view. B, family Microhedylidae, *Microhedyle cornuta*, dorsal view. C, family Ganatidae, *Paraganitus ellynnae*, dorsal view. (A, after Arnaud *et al.* 1986) [R. Plant]

but have a rudimentary velum at one stage of development (Arnaud *et al.* 1986). One species is thought to be from Sri Lanka, the others are from the east and west coasts of the Atlantic from Brazil to Norway (Salvini-Plawen 1991). The genus *Rhodope* also occurs at Guam in the western Pacific (Carlson & Hoff 1981). All except *R. veranyi* are known from only one or very few specimens.

A single specimen of *Rhodope*, found crawling on intertidal *Zostera* on a reef flat in Westernport, Victoria (Burn 1990), indicates the presence of this molluscan order in the Australian marine fauna.

Order SACOGLOSSA

The order Sacoglossa is a circumscribed group of three superfamilies and 12 families, containing some 200 known species. Sacoglossans exhibit two common features: an almost exclusively herbivorous habit, and the possession of a uniseriate radula in which the older, often abraded, teeth are retained in a special sac (hence the name of the order). The teeth are most often blade-like, and are used to puncture individual plant cells so that the fluid contents may be sucked out and swallowed. Dissociated chloroplasts from the alga may be retained and farmed in the cells of the digestive gland, where they persist for one or more weeks (Clark *et al.* 1990). The few carnivorous species feed upon the eggs of other opisthobranchs. One of these species lacks a functional radula.

The primitive sacoglossans have a relatively strong external shell, either bulliform or bivalved, into which the animal can withdraw. Others have only a reduced shell covering the visceral mass. The shelled forms have a pallial gill, and only one female genital aperture. The visceral loop behind the pharynx is usually long,

with ganglia, and is slightly streptoneurous. The more advanced, shell-less sacoglossans have either parapodial lobes or cerata along each side of the body, but these may be secondarily lost. The cerata, if present, generally contain a branch of the digestive gland, and sometimes of the albumen gland, but lack cnidosacs. The shell-less sacoglossans have a short visceral loop, with three ganglia in the Elysioidea and two or three ganglia in the Limapontioidea. There may be one, two, or exceptionally, three, female apertures.

The sacoglossan body-shape may be limaciform, aeolidiform with dorso-lateral cerata, or flattened and leaf-like. The head bears a pair of digitiform auriculate rhinophores, sometimes partly bifurcated and occasionally reduced or absent. Oral tentacles are usually small, and used for grasping algal stems during feeding. There are neither jaws (except in *Platyhedyle*) nor gizzard plates. The pharynx often has a posterior ventral pharyngeal crop, and there may be an oesophageal diverticulum anterior to the stomach. The anus may be dorsal, on the right side, or posterior. The pericardial heart is absent in exceptional forms. The digestive gland is often much branched, the branches extending into the head, rhinophores, foot and cerata. The reproductive system is hermaphroditic, with a closed internal vas deferens, and the penis is often armed with a tubular chitinous stylet, which in many species use to transfer sperm hypodermically, not vaginally.

The fossil record of sacoglossans with bivalved shells dates from the Eocene of Europe. They are known from the Middle Miocene and Pliocene of southern Australia. There are no records of fossil bulliform sacoglossan shells. The great similarity of *Ascobulla* and the cephalaspidean *Cylindrobulla* may indicate the evolutionary origins of the Sacoglossa. The fossil record from the Eocene to the present day shows that sacoglossans have maintained strong phylogenetic integrity during this time.

Between 1850 and 1900, most knowledge of sacoglossans came from Europe and the Mediterranean region. The shelled and shell-less forms were first grouped together in 1876, but were not readily accepted as a distinct group. Most were, for a long time thereafter, still associated with other opisthobranch groups – the oxynooideans with the Cephalaspidea, and elysioideans and limapontioideans with the aeolid Nudibranchia. In fact, until the discovery in 1959 of live juliid oxynooideans, the so-called bivalved gastropods, these were classified as anomalous bivalves! Since then, however, knowledge of the order as a whole has advanced at a rapid rate, largely due to the work of Er. and E. du B.-R. Marcus in the Americas, Gonor in California, Gascoigne in Europe, the Mediterranean and North America, Baba in Japan, Clark and his colleagues in Florida and the Caribbean, and Jensen in Europe, Florida, Hong Kong and Australia. The reviews of sacoglossan diets and alimentary systems by Jensen (1980, 1991), and the survey of functional kleptoplasty (= symbiotic

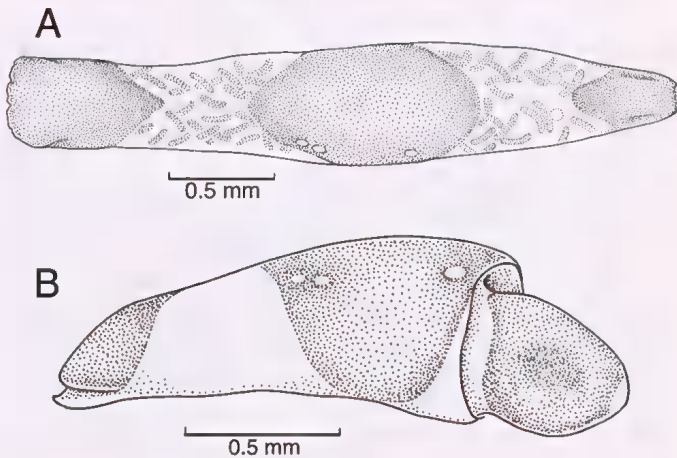


Figure 16.43 Family Rhodopidae. *Rhodope* sp., from Westernport, Victoria: A, crawling animal, dorsal view; B, animal in repose with anterior part of body retracted, right lateral view. (After sketches by R. Burn) [R. Plant]

chloroplasts of earlier writers) by Clark *et al.* (1990) are essential reading for anyone working on the order. There is a substantial literature on the taxonomy, systematics, biomorphology and biology of the species in the order.

The classification used here is an amalgam of recently proposed schemes (Marcus, Ev. 1982; Gascoigne 1985), but it seems likely that further refinements will be made in the future. The status of the higher taxa is still contentious, with some authors maintaining the Sacoglossa as an order with two suborders, Conchoidea (with shell) and Aconchoidea (without shell). Such a scheme sits uncomfortably within the recently proposed caenogastropod and heterostroph classification (Ponder & Warén 1988), and still more recent arrangement of Ponder & Lindberg (1996) following which the Opisthobranchia as a whole is accorded only ordinal status (see Table 15.1). The Sacoglossa is here given ordinal rank, and each of its three major divisions is recognised at superfamily level. The classification advanced by Minichev & Starobogatov (1978, 1979b), in which the Sacoglossa is divided into two superorders, and each family elevated to superfamily status, has not met with acceptance.

Recently, a number of important contributions to the Sacoglossa, including data relevant to the Australian fauna, have been published by K.R. Jensen. She has reviewed the anatomy of some Indo-Pacific Elysiidae and discussed the generic divisions within the family (Jensen 1992). Also, ten new species have been described from Rottneest Island and Darwin Harbour, and other species added to the Australian fauna and redefined at generic and specific level (Jensen 1993a, in press). Other papers have dealt with sacoglossans as specialist herbivores (Jensen 1993b); the evolution of their buccal apparatus (Jensen 1993c); and morphological adaptations and radular tooth plasticity (Jensen 1993d).

Superfamily OXYNOOIDEA

Sacoglossans with shells, either coiled or bivalved, are accommodated in Oxynooidea. The shells may be large, allowing the animal to withdraw completely, or considerably smaller, protecting only the visceral mass. Those groups with large shells include burrowing cephalaspidean-like forms with a short foot such as recurs commonly in the Elysiioidea and rarely in the Limapontioidea. The Oxynooidea also includes the curious bivalved gastropods, an evolutionarily successful side-branch with a fossil record dating back to the Eocene. The nervous system of Oxynooidea is less concentrated and less cephalised than in the other superfamilies, with generally a long triganglionate visceral loop showing traces of streptoneury. The pharynx generally has a large posterior ventral pharyngeal crop, and more distally, an oesophageal diverticulum. The penis is unarmed, but it may be long and cuticularised, with accessory knobs and flanges. In the more primitive forms, the single female genital aperture has an anteriorly directed external oviducal groove. Oxynooideans are all obligatory feeders on the green alga *Caulerpa*.

Family Volvatellidae

The family Volvatellidae comprises two primitive sacoglossan genera with coiled shells, into which the body can be withdrawn completely (Fig. 16.44). One genus, *Ascobulla*, shows similarities to the cephalaspidean genus *Cylindrobulla*; the resemblances are probably plesiomorphic. The other genus, *Volvatella*, which, though not resembling *Cylindrobulla* in shell characters as closely as *Ascobulla*, sometimes has a broad radular tooth that could easily have been derived from the even broader tooth of a *Cylindrobulla*-like ancestor. Both genera are widespread in tropical and temperate seas, but because of their cryptic colouration and secretive (often burrowing) habits, are rarely found in any number.

The shells are thin and 'elastic', more or less cylindrical, but much broader in *Volvatella* (Fig. 16.44B) than *Ascobulla*, and usually narrower anteriorly. There is a strong yellowish periostracum and a thin, white, inner calcareous layer of shell. The aperture is rather small and rounded, more anterior or antero-ventral than ventral,

with a very narrow posterior extension to the apex or beyond. The outer lip, straight in *Ascobulla*, overlaps the last whorl, and apically forms a long sutural slit level with the protoconch. In *Volvatella*, the outer lip is strongly curved, overlaps the last whorl to a lesser degree, and projects beyond the protoconch to form a short conical to elongate cylindrical spout. The shell can reach up to 24 mm in length in *Volvatella* (Souverbie 1861), and about 10 mm in *Ascobulla*.

The neck and head extend well beyond the shell in *Ascobulla*, and to a lesser extent in *Volvatella*. The foot is very short. Two flattened lobes, separated by a median furrow and partially free posteriorly, form the cephalic shield in *Ascobulla* (Gosliner 1987a; Jensen & Wells 1990). Eyes are not visible in *Ascobulla*. *Volvatella* has four lobes on the head, possibly anterior and posterior remnants of the flattened lobes of the presumed *Ascobulla/Cylindrobulla* ancestral form. The anterior and posterior pairs resemble oral lobes and rhinophores, respectively. Eyes may be visible behind the latter. The body is usually milky-white (Gosliner 1987a), and the orange digestive gland is visible through the mantle and shell. In some *Volvatella* species, the animal and shell mantle are orange in colour, and the dark reddish-orange digestive gland shows through the shell. Other species have a greyish visceral mass with a paler, opaque digestive gland.

The transverse adductor muscle in volvatellids is inclined or diagonal at about the first quarter of the shell length. This controls the closing of the outer lip of the shell, which occludes entry of sand particles into, and aids flushing of, the mantle cavity. It may also facilitate movement through the substratum (Clark 1982a). A long band of parallel branchial lamellae traverses the dorsal and left side of the mantle cavity. A low ciliated ridge and hypobranchial gland lie dorsally behind the gill, and ventrally on the visceral mass. An infrapallial lobe fills the narrow part of the aperture. The anus opens high on the visceral mass behind the level of the gill. The female aperture lies below and in front of the adductor muscle, on the right side of the body.

The pharynx is small and barrel-shaped in *Ascobulla*, and the pharyngeal crop is short and broad with a single lumen; a labial cuticle may be present in the short oral tube. In *Volvatella*, the crop is spherical, six to eight times larger than the pharynx, and has paired slender lumina. A pair of salivary glands enter the pharynx beside the oesophagus. The radular teeth are slender and blade-like with fine lateral denticles in *Ascobulla*; those of *Volvatella* are much broader and coarsely denticulate laterally. The oesophagus dilates a short way behind the pharynx, but does not form an oesophageal diverticulum in all species.

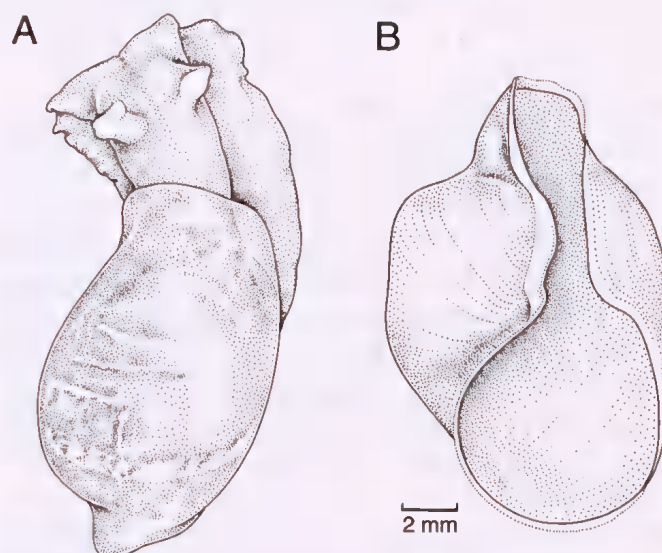


Figure 16.44 Family Volvatellidae. *Volvatella vigourouxii*: A, animal, dorsal view; B, shell, apertural view. (A, after photograph by N. Coleman) [R. Plant]

The circumoesophageal nerve ring usually encircles the oesophagus behind the pharynx. The cerebropleural ganglia show various degrees of concentration, but usually the commissures are distinct between the cerebropleural and pedal ganglia. The visceral loop is long and slightly streptoneurous with the supra-intestinal ganglion more dorsal than the subintestinal; their position along the visceral loop may vary between species. Parietal ganglia may be present also.

Volvatellids have an ampulla opening into the spermatoduct at its junction with the hermaphrodite duct. The long spermatoduct widens and curves before dividing. The male branch immediately becomes prostatic, then runs forward as an internal closed vas deferens to the elongate folded penis in its pouch within the right side of the neck. The penis usually has a flexible stylet, and a swelling may be present within the lower penis as a sperm reservoir or ejaculatory pouch. The long curved or convoluted vagina links the female aperture and the large bursa copulatrix. In *Ascobulla* there is a smaller seminal receptacle at mid-length. A ciliated oviducal groove runs forward along the right side from the female aperture to forward of the male aperture.

Ascobulla species lay a long ribbon of egg capsules, each about 200 µm in diameter. Crawling young emerge from eggs of the Caribbean *A. ulla*, but young of the southern Australian *A. fischeri* emerge as planktotrophic veligers (Clark & Jensen 1981; Jensen & Wells 1990). *Volvatella* species lay smaller capsules about 100 µm in diameter and development of the eggs is planktotrophic (Clark 1982a). Seven species have been assigned to *Ascobulla* (Jensen & Wells 1990), but they remain poorly differentiated from one another and from species of the cephalaspidean genus *Cylindrobulla*. The southern Australian *A. fischeri* was described in some detail by Jensen & Wells (1990), and suggestions made as to possible synonyms. *Ascobulla fischeri* has been found in association with *Caulerpa brownii* along the Victorian coast (R. Burn personal observation). Species have been described from the Mediterranean, the Persian Gulf, Sri Lanka, Japan and California, but the most detailed information is available for *A. ulla* from the tropical west Atlantic (Marcus, Ev. & Marcus, Er. 1956a; Marcus, Ev. 1972c); details of ecology, burrowing behaviour and feeding methods are provided by De Freese (1987), Jensen (1981b), and Thompson *et al.* (1985).

Seventeen species of *Volvatella* are known, of which only *V. bermudae* is not from the wider Indo-Pacific. *Volvatella ventricosa*, a species with a short spout, is known from southern Western Australia (Jensen & Wells 1990) where it was found living on *Caulerpa racemosa*. A second short-spouted species, *V. australis*, has been described from the Darwin area of the Northern Territory (Jensen in press). The long-spouted *V. pyriformis* has been recorded from 'Queensland' and Lizard Island (Hedley 1910a, 1910b; R. Burn personal observation). *Volvatella cincta* has been found alive at Cocos-Keeling Islands (Maes 1967). Other as yet unidentified species, of which at least two have orange bodies, have been found along Australia's warmer coastlines. The Japanese *V. kawamurai* is the only species for which the anatomy has been described fully (Baba 1966). Some anatomical information about other species is given by Evans (1950), Kay (1961), Burn (1966b), Hamatani (1972, 1976), Clark (1982a), Gascoigne (1985) and Jensen & Wells (1990).

All volvatellids live on *Caulerpa*, with *C. racemosa* being the favoured food for many species. They either burrow through the sandy substratum to find and eat the rhizoids, or crawl up the stipes to feed on the vesicles (Jensen 1981b). In the green-shelled *V. bermudae*, non-functional, symbiotic chloroplasts are present in the digestive diverticula (Clark 1982a). Volvatellids are mostly shallow subtidal animals; presumably their bathymetric distribution is restricted by the light requirements of their food algae.

Family Oxynoidae

The family Oxynoidae comprises only 10 or 11 species worldwide, placed in four genera, three well-founded and one doubtful. Oxynoids appear to form a lateral branch of the line that gave rise to the Volvatellidae, but are distinguished by an increase in body size and the formation of parapodial lobes, a reduction in shell size and loss of the capacity to withdraw for protection, a centralisation of the nervous system, and loss of the ability to burrow. To the human eye, oxynoids are extravagantly coloured and flamboyantly shaped, but they are extremely well camouflaged when on their food algae (Pl. 34.3). At times, the genera have been separated into two families, Oxynoidae and Lobigeridae, but with the recognition of the genus *Roburnella* (Fig. 16.45; Pl. 37.2) which has characteristics of each group, the more conservative classification has been adopted again. The southern African *Lophopleurella* (Thiele 1912, as *Lophopleura*), described as having smaller, smooth parapodia without lobes, is probably a species of *Lobiger*, its lobes autotomised.

The thin oxynoid shell covers the visceral mass only. In *Oxynoe*, it is broadly bulloid, the aperture is large, the upper part of the outer lip overlaps the small last whorl, and the protoconch is level with the apex. In *Roburnella*, the shape is elongate-ovoid, the upper part of the outer top lip is well separated from the last whorl which is small and compact, and the protoconch is apical. In *Lobiger*, and the poorly known *Lophopleurella*, the shell is elongate-oval and almost saucer-like, the aperture is very large, and the last whorl is reduced to a thickened marginal roll containing the protoconch. A pale yellowish periostracum is present. Mantle pigmentation can be seen through the shell in life; in some *Lobiger* species, six to eight green, blue or black lines mark the mantle.

The oxynoid animal is invariably pale green to dark brownish-green, often with blue, green, brown, yellow or white spots (Pl. 34.3; Gosliner 1987a). Iridescent blue ocelli are often present in *Oxynoe*. There is a pair of auriculate rhinophores on the head (Fig. 16.45), which are greatly expanded in *Lobiger* from the lower front edge into an angular lobe. The eyes are prominent on the sides of the neck behind the rhinophores. The neck is short and thick, and swells into the visceral mass within the shell. The tail is long and slender in *Oxynoe*, shorter and broader in *Lobiger*, and short and broad with a rounded tip in *Roburnella*. The parapodia rise from the lower sides of the body, and in *Oxynoe* are rather small with an irregular margin, and conical or branched papillae on the outer face. In *Roburnella* and *Lobiger*, each parapodium has two elongate lobes – in the former small, smooth and spoon-shaped; in the latter large, marginally crenulate to deeply notched, and papillose on the outer face. Caudal autotomy in *Oxynoe*, and parapodial lobe and caudal autotomy in *Lobiger* has been described (Gonor 1961b).

Like the other shell-bearing sacoglossans, the mantle cavity contains a dorsal band of parallel branchial lamellae, behind which lies the hypobranchial gland. In *Oxynoe*, the heart is far to the left and the anus opens postero-laterally on the right. In *Lobiger*, the heart and anus are nearer the median line, with the latter opening posteriorly. The female aperture lies on the right side of the body within the protection of the anterior part of the shell.

The buccal bulb takes two forms. In *Oxynoe*, and *Roburnella* to a lesser degree, there is a large pre-pharyngeal muscular oral tube (Souleyet 1850; Ihering 1892; Burn 1966b, Marcus, Ev. & Marcus, Er. 1970), observed in *Oxynoe* to be protrusible and used to grasp its algal food (Jensen 1980; Jensen & Wells 1990). A post-pharyngeal, broad, thick, U-shaped crop with a single lumen is attached ventrally to the muscular, globular pharynx. In *Lobiger*, a pair of muscular thickenings is present instead of an oral tube, the pharynx is slender and elongate, the radular ascus projects ventrally, and an elongate, winding crop with two slender lumina is attached to the posterior left wall of the pharynx. The salivary glands have long, thick ducts with ramose ends in *Oxynoe*, or short ducts with lobulate or ramose ends in *Lobiger* and *Roburnella*. A sausage-shaped oesophageal diverticulum,

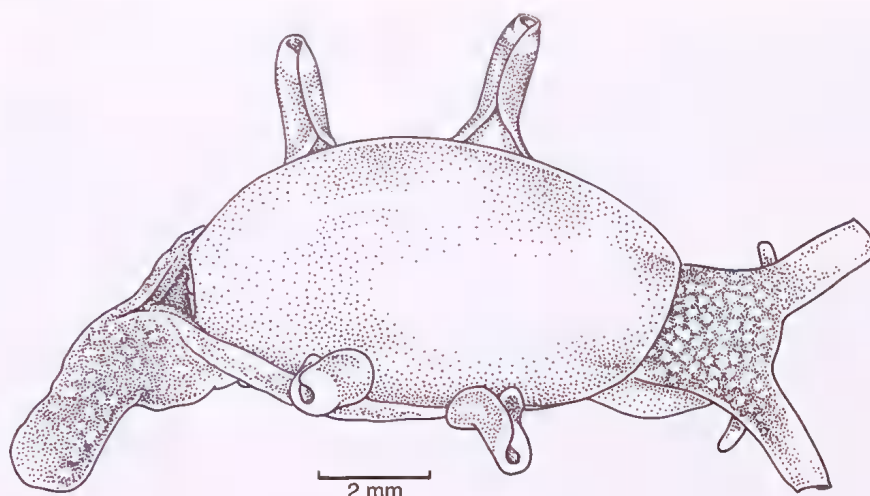


Figure 16.45 Family Oxynoidae. *Roburnella wilsoni*, dorsal view. (After sketch by R. Burn)

[R. Plant]

either smooth or warty, opens to the oesophagus some way behind the pharynx. The radular teeth are broadly blade-shaped with fine lateral denticles for almost the whole tooth length in *Oxynoe*. In *Lobiger* and *Roburnella*, the teeth are slender, usually double-notched in the rounded tip, and long or short, fine, lateral denticles may be present on all or some teeth.

The highly concentrated circumoesophageal nerve ring encircles the oesophagus behind the pharynx. All three genera have a very short visceral loop immediately behind the cerebral ganglia. In most species, the supra-intestinal and visceral ganglia are large and the subintestinal ganglia small. The presence of the latter is not reported for some species.

The ampulla of the hermaphrodite duct is long and winding. The male branch first passes through the prostate gland, then leads forward as a slender, internal closed vas deferens to the ejaculatory duct at the base of the penial papilla lying in its pouch behind, and ventral to, the right eye. The penis is simply conical and unarmed in *Lobiger*, with two or three sharp points to blunt knobs in *Oxynoe*. The long rather straight vagina opens just within the female aperture. At the inner end, it enters the larger spherical bursa copulatrix. In *Lobiger*, the smaller seminal receptacle enters the vagina at mid-length (Pelseneer 1894; Bergh 1900). The same condition is reported for *Oxynoe* (Souleyet 1850; Ihering 1892), but needs to be verified because recent studies show an inner connection between the vagina and large oviduct, with the seminal receptacle positioned mid-way along the small oviduct, where it probably functions as a fertilisation chamber (Sanders-Esser 1980, 1984).

At present, only three oxynoid species are recognised in Australian waters. *Oxynoe viridis* is relatively common throughout its wide distribution along both tropical and temperate coastlines, with the possible exception of Tasmania. The name may hide a complex of species (Gosliner 1987a). The anatomy of specimens from southern Western Australia has been described recently (Jensen & Wells 1990). *Oxynoe viridis* eats a variety of *Caulerpa* species, and has been found in association with *C. brownii*, *C. cactoides*, *C. geminata*, *C. racemosa*, *C. scalpelliformis*, and *C. remotifolia*. *Lobiger viridis* is less common but widespread through the tropical Indo-Pacific (Burn 1966b). It is usually found in association with *C. racemosa*. Six to eight green, blue or black lines mark the mantle of *Lobiger viridis* and its Caribbean cognate *L. souverbii*, and it has been suggested that they are one and the same (Kay 1964, 1979). However, the very large, deeply indented parapodial lobes of *L. viridis* readily distinguish it from *L. souverbii* in which the lobes are marginally crenulated. The single species of *Roburnella*, *R. wilsoni* (Fig. 16.45; Pl. 37.2), is distributed from both coasts of Bass Strait westward to south-western Western Australia (Burn 1979, 1989; Jensen 1993a). It is associated with *Caulerpa brownii*, *C. scalpelliformis* and *C. remotifolia*.

In Australia, *Oxynoe viridis* lays some 30 000 small eggs of 60 µm diameter in one spawning; these hatch in 6–7 days as planktotrophic veligers (Rose 1985). In the Caribbean, *O. antillarum* lays fewer equally small eggs which emerge as planktotrophic veligers (Clark & Goetzfried 1978) whereas *O. azuropunctata* lays even fewer but much larger eggs that produce lecithotrophic veligers (Jensen 1980; Clark & Jensen 1981). *Lobiger souverbii* lays small eggs and has planktotrophic veligers (Clark & Jensen 1980). *Oxynoe olivacea* from the Mediterranean and eastern subtropical Atlantic lays 90 to 100 eggs per centimetre of egg ribbon, with large eggs 250 µm diameter in capsules 500 µm across (Ortea 1981).

On the basis that both have three visceral ganglia, it has been suggested that the Elysiidae evolved from the Oxynoidae (Boettger 1963). However, it is now known that three visceral ganglia occur in other shelled, as well as aeolidiform, sacoglossans, which weakens this argument. It has also been pointed out that the digestive gland in the Oxynoidae occupies only the shell mantle, whereas it extends to the very edge of the parapodia in the Elysiidae (Jensen 1981a). On the basis of the unusual and very complicated feeding methods of *Oxynoe*, it has been suggested that the family represents an evolutionary 'dead-end' (Jensen 1981b).

Information on the effects of algal filament diameter on food preference and growth; on autotomy and regeneration; and on toxicity of hypobranchial discharges can be found in Jensen (1981a), Warmke & Almodovar (1972), and Lewin (1970), respectively. Early studies on *O. olivacea* and *L. serradifalci* from the Mediterranean are still valuable references (Souleyet 1850; Ihering 1892; Pelseneer 1894).

Family Juliidae

The ancient but evolutionarily successful juliid sacoglossans all have a two-valved shell, and are commonly known as bivalved gastropods (Fig. 16.46; Pl. 34.1). Prior to 1959, the fossil and Recent members of the family were regarded as enigmatic bivalves. In that year living specimens, found in numbers on the shores of Japan, were described as sacoglossans with two-valves (Kawaguti & Baba 1959). Other living species were soon discovered in southern Australia (Burn 1960a, 1965), Baja California (Keen & Smith 1961), the Caribbean (Edmunds 1963), Hawaii (Kay 1964), and later on, in Guam (Carlson & Hoff 1971), India (Sarma 1975), Japanese waters (Kawaguti 1981; Kawaguti & Yamasu 1982), and southern Africa (Gosliner 1987a). The named fossil species were reassessed and new species were described from Australia, Indonesia, Japan, Germany and Poland by Ludbrook & Steel (1961), Boettger (1963), Janssen (1979), Baluk & Jakubowski (1968) and Mimoto (1984). Fossil species date back to the Middle Eocene.

The family can be divided conveniently on the basis of differences in the shells. In the Juliinae, the shell is up to 6 mm long, solid, tumid, cordate in shape, with a heavy knob and socket hinge, and a very small protoconch which is often dislodged in adult and dead shells. It is generally dark brownish-green in colour, and may have bright and dark green radial bands over the whole or anterior half of each valve. In the Bertheliniinae, the shell is up to 10 mm long, thin, slender, lenticular in shape, with a very weak hinge sometimes with obsolete teeth, and a large protoconch retained in adult and dead shells. It is generally yellowish-green in colour, and may have radial stripes corresponding to radial patterns of the mantle.

The juliid animal is light to dark green in colour, sometimes with lighter bands on the rhinophores and neck. The mantle is visible within the shell in the Bertheliniinae and may show yellow bands or white spots radiating out from the umbos, or a few black horizontal lines, or much brown, more or less horizontal stippling. The crawling animal is about twice the length of the shell, and the pointed tail rarely projects posteriorly beyond the shell. The animal can withdraw completely into the closed valves. On the head, a pair of auriculate, generally cylindrical, rhinophores diverge antero-dorsally, a pair of oral lobes occurs beside the mouth, and paired eyes are close together on a small raised prominence about halfway (*Berthelinia*) along the top of the neck, or closer to the rhinophores (*Julia*; Fig. 16.46). The neck is usually long and slender, but is short and thick in *Midorigai*.

The visceral mass is mostly contained within, and attached to, the left valve. The space between the viscera and the right valve forms the mantle cavity. The gill comprises a band of parallel lamellae suspended from the right mantle (*Berthelinia*) as well as the top of the visceral mantle (*Julia*). The anus opens high up on the visceral mantle, a little behind the gill. Also behind the gill, a strongly ciliated ridge accompanying the hypobranchial gland projects from both mantles. A strong, transverse adductor muscle at the anterior third of the visceral mass controls the closing of the shell valves; its points of attachment can be seen easily through the thin shells of the Bertheliniinae. The mantle glands that secrete the shell are two layered in the thin-shelled Bertheliniinae, and three layered in the thick-shelled *Julia*.

The alimentary canal commences with a large muscular pharynx. In *Berthelinia caribbea* and *Edentellina typica*, the dorsal wall of the pharynx expands to form a buccal pouch almost as large as the pharynx (Edmunds 1963; R. Burn personal observation). Attached to the rear of the pharynx are a pair of pharyngeal crops and a pair of salivary glands. The crops are widely separated, club-shaped, and about as long as the pharynx in the Bertheliniinae; they are cylindrical and about six times as long as the pharynx in *Julia*. The salivary glands are long and slender in the Bertheliniinae, and much longer in *Julia*. A large sac or diverticulum branches from the oesophagus some distance behind the pharynx. The blade-like radular teeth are generally finely denticulate along each side. In some species, the tip of the tooth is notched as well; others have no lateral denticles.

The circumoesophageal nerve ring encircles the oesophagus behind the pharynx. The cerebropleural ganglia are concentrated more or less in the dorsal and lateral regions. The distance from the visceral and cerebral ganglia and the supra-intestinal and subintestinal ganglia on the long, somewhat streptoneurous, visceral loop varies between species. According to Baba (1961), the long visceral loop demonstrates an ancestral affinity with the Cephalaspidea.

The male branch of the reproductive organs includes a swollen glandular prostatic section, an internal closed vas deferens, and a large tapering penial papilla held within a pouch on the anterior right side of the neck. A seminal pouch may be present at the base of the male branch. The penis is generally unarmed, but some Bertheliniinae have a flexible style with peculiar twists, flanges and prongs to aid copulation (Grahame 1969; Gascoigne 1974a). The ovoid bursa copulatrix connects to the lower large oviduct by way of a long, slender, straight vaginal duct (*Julia*). In the Bertheliniinae, the vaginal duct continues further to the smaller rounded seminal vesicle. The female aperture lies behind the level of the adductor muscle, and from it runs a shallow ciliated oviducal groove along which eggs are conveyed during oviposition.

Juliids lay small, flat, sausage-shaped packages of eggs on or near their algal food. The eggs may be small (100–150 μm) and number up to 2000 per spawning (*Julia*), or larger (250–380 μm) and 11 to 470 per spawning (Bertheliniinae). *Tamanovalva limax* is easily maintained in the laboratory and lives for up to nine months; it may spawn 40 to 50 times during its lifetime, and lays about 5000 eggs (Kawaguti & Yamasu 1960). *Julia japonica* lives just as long, and can spawn every other day at the height of the spawning season (Kawaguti & Yamasu 1966). *Berthelinia caribbea* lives only three months, spawns continuously from about day 37, and lays about 1500 eggs in masses containing 11 to 100 capsules 300 μm long (Grahame 1969). Its development is lecithotrophic (Clark & Jensen 1981).

Juliids live in all the tropical and temperate seas of the world except the eastern Atlantic and Mediterranean. They are restricted in habitat and food to species of the lower intertidal and subtidal green alga, *Caulerpa*. They may be exceptionally common locally but difficult to find because of their cryptic colouration and tenacity. *Julia* and *Tamanovalva* both occur on the Great Barrier Reef (Hedley 1920; R. Burn personal observation); and *J. exquisita* has been found at Cocos-Keeling Islands (Maes 1967). Three genera, each with one species, are found along the south-eastern temperate coastline; *Edentellina* is restricted to *Caulerpa brownii*, *Midorigai* occurs only on *C. simpliciuscula*, whereas *Tamanovalva* is found on *C. scalpelliformis*, *C. geminata* and *C. cactoides* (Burn 1989). *Berthelinia rotnesti* and several undescribed species are known from south-western Australia, and another from Norfolk Island (Jensen 1993a; R. Burn personal observation). *Julia* is represented as a Middle Miocene fossil in the Tertiary beds of southern Australia (R. Burn personal observation), and *Berthelinia* by a Pliocene species (Ludbrook & Steel 1961).

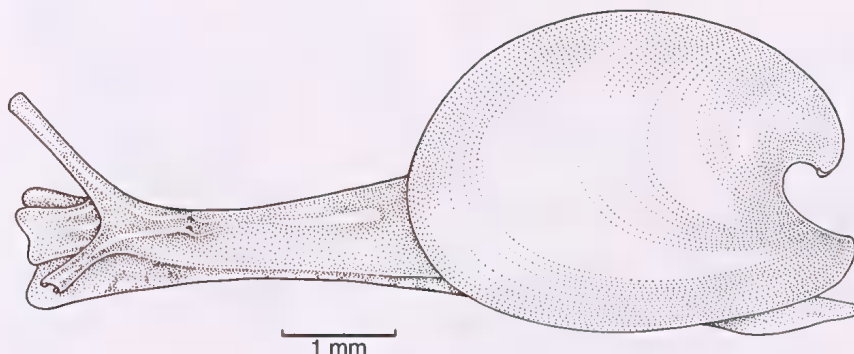


Figure 16.46 Family Juliidae. *Julia japonica*, dorso-lateral view. (After Kawaguti 1981)

[R. Plant]

The systematics of the Juliidae are poorly understood (Boettger 1963; Kay 1968; Jensen 1993a, in press), and the status of some of the genera mentioned above is uncertain. The genera *Berthelinia* and *Tamanovalva* appear to be identical, the former name having been applied to a fossil, the latter to a Recent species (Jensen 1993a).

The best known species are the Japanese *Tamanovalva limax* and *Julia japonica*, and the tropical west Atlantic *Berthelinia caribbea*. In a long series of papers published between 1959 and 1968 (listed by Yamasu 1968), Kawaguti & Yamasu, either alone or jointly, described aspects of mantle structure and shell formation, development of the adductor muscle, nervous system and alimentary canal, anatomy and histology, general biology, feeding and fertilisation. Further details of anatomy, spawning and development, radular teeth, and nervous systems are found in Baba (1961), Wisely (1962), Edmunds (1963), Grahame (1969), Gascoigne & Sartory (1974), Sarma (1975) and Gascoigne (1985).

Superfamily ELYSIOIDEA

Elysioideans are those shell-less sacoglossans with parapodial folds along each side of the body, and, in those taxa without parapodia, in which the sole of the foot is transversely divided into a short anterior 'ancestral' sole and a longer 'visceral' sole. The parapodia may be elaborated by increased folding or by the addition of lobes or dendritic papillae along the margins. The parapodia are usually folded over the dorsum to meet in the centre line. Dorsal vessels usually radiate from the pericardium. The rhinophores are auriculate, but may be reduced or absent. The centralised circumoesophageal nerve ring has three ganglia along the short visceral loop. The pharynx seldom has a posterior ventral pharyngeal crop. The penis usually lacks an apical stylet; and copulation is generally reciprocal, but rarely hypodermic to any part of the body. There may be one or two female genital apertures.

Elysioideans feed primarily on green algae. A few species feed on diatoms, brown algae, and seagrasses.

Elysioidea comprises five families, the Plakobranchidae, Elysiidae, Boselliidae, Platyhedylidae and Gascoignellidae. The inclusion of the Platyhedylidae and Gascoignellidae, both without parapodia and rhinophores, among the elysioideans might be regarded with some scepticism. However, both families have the transversely divided sole and short triganglionate visceral loop in common with the rest of the superfamily, and their higher separation within the Sacoglossa is considered unwarranted.

Family Plakobranchidae

The family Plakobranchidae is monotypic (Jensen & Wells 1990). *Plakobranchus ocellatus* (Fig. 16.47), despite its common occurrence, large size of 65 mm or more, and the fact that it was the first sacoglossan known from the Indo-West Pacific (Hasselt 1824), remains relatively poorly known. Some colour forms are extremely distinctive. Bergh described it under different names from different localities, but could not decide whether there was one (Bergh 1887, 1902a) or many species (Bergh 1871, 1871–1873, 1888a, 1905a). Others added further names (Gould 1852; Pease 1860, 1871) so that in all 14 names have been given to what is now regarded as one species.

Though variable in colour, *P. ocellatus* always has brown and blue spots encircled by white and/or black rings on a pale greenish to dark brownish body. The rhinophores are generally tipped with blue or purple tints. The parapodia, when unfolded, and the dorsal surface are dark green or brown. The sole and ventral surface have only black spots or rings on a paler body colour.

The body closely resembles a broad, parallel-sided, compressed *Elysia* with large, laterally directed rhinophores (Fig. 16.47). The head is broad, short, and continues back as a tapering neck to well within the parapodia. The posterior body is roundly truncate. The eyes are close together on the top of the head, in a little dome as in bertheliiniids rather than side by side as in *Costasiella*. The foot is

wide anteriorly with angular corners, very short, and separated from the posterior viscera by a distinct transverse groove which continues up each side of the body. The ventral surface of the posterior viscera is not adapted for crawling. The parapodia are extremely wide and thin, and on the outer side are not markedly set-off laterally from the ventral surface; on the inner side there are numerous longitudinal lamellae, 0.5–1.5 mm high, which are filled by branches of the digestive gland. The pericardium lies behind the neck, and extends rearwards as a narrowing renopericardial ridge before dividing into several lamellae about mid-length. The anus opens on the right side of the pericardium.

The small pyriform pharynx comprises a slender oral tube anteriorly and a thick hemispherical crop postero-ventrally. The salivary glands are warty and have long ducts. A thick oesophageal diverticulum lies well behind the pharynx. The slender radular teeth are elongate basally, and bear coarse squarish lateral denticles as in *Volvatella*. The centralised nervous system, consisting of the nerve ring and triganglionate visceral loop, is almost as big as the pharynx; the cerebral, pedal and visceral ganglia are equal in size, and the supra-intestinal and subintestinal ganglia are much smaller. The stout penis has a long, strongly curved, cuticular stylet at the tip, and a coiled ejaculatory duct within its base. The bursa copulatrix at the end of the long vagina opens to the inner end of the large oviduct. The hermaphroditic duct of the ampulla is long and winding before it branches into the male and female ducts. The albumen and prostate glands are spread throughout the posterior viscera, and lie near the ventral surface. A pair of large copulatory bursae are present behind the pericardium (Jensen 1992).

Plakobranchus is allied to *Elysia*, but *Elysia* lacks longitudinal lamellae on the dorsum. *Pattyclaya*, another elysioid, does have dorsal lamellae (Marcus, Ev. 1982; Jensen & Wells 1990), but these are transverse, not longitudinal. Coarsely denticulate radular teeth do not occur in *Elysia*, though there is some similarity to those of *Thuridilla*. Also, the penial stylet of *Plakobranchus* is not known in elysioid genera. Although maintained as a separate family here, Plakobranchidae was united very recently with the family Elysiidae (Jensen 1992, in press).



Figure 16.47 Family Plakobranchidae. *Plakobranchus ocellatus*, dorsal view. (After photograph by N. Coleman) [R. Plant]

Plakobranchus ocellatus occurs throughout northern tropical Australia. It has been reported from eastern Africa and the Red Sea to Hawaii and Tahiti, and from the southern coast of China to the Great Barrier Reef. In the Solomon Islands, it is one of the conspicuous opisthobranchs inhabiting the inner part of the reef flat (Miller 1969), where it is found on lumps of coral rock covered with *Enteromorpha*. Elsewhere it is found in sandy and silty areas, where it spawns all year round. Its iridophores (blue spots), pigment and mucous cells, muscular structure, and algal symbiosis have been studied by Kawaguti & Kamishima (1964), Kawaguti, Yamamoto & Kamishima (1965), Kawaguti, Kamishima & Nakamura (1966) and Kawaguti (1968). It is preyed upon by *Gymnodoris striata* (Johnson & Boucher 1983).

Family Elysiidae

The family Elysiidae (Fig. 16.48), the largest family in the Sacoglossa, contains all species with lateral parapodia except those accommodated in the Plakobranchidae. The lateral parapodia may be intricately convoluted marginally, as in *Tridachiella*, or low and thick, as in *Elysiella*. There are at least 75 described species, many synonyms, and many species awaiting description. The nominate genus, *Elysia*, comprising some 60 species, can be divided into obvious species groups, for which a number of generic names (presently regarded as synonyms) are available. Elysiids are common all round Australia except for Tasmania, and include many species of *Elysia*, fewer of *Thuridilla*, and one each of *Pattyclaya* and *Elysiella*.

Elysiids are generally green in colour, and some mimic their host food precisely. However, the range of colours is wide, from dull cream, through bright yellow, green of all shades, brown and reddish-brown, to blue and almost black. Some species have white, yellow, orange, red, blue or black bands and stripes along the parapodial margins, and others have iridophore-like blue patches laterally. They are generally very soft and smooth, though a number of species have papillae on the rhinophores, head and outer side of the parapodia. In one Lizard Island species, projecting bunches of minute spicules tip the papillae lining the anterior edge of the rhinophores and oral lobes (R. Burn personal observation).

Adult elysiids range in length from 5 mm to almost 100 mm, with most less than 40 mm. They have a pair of wing-like parapodia which are usually folded up on the dorsal side, meeting more or less in a wavy line mid-dorsally (Fig. 16.48B). The lower edges of the parapodia are usually delimited from the lateral edges of the foot. The two rhinophores on the head are smooth and tapering in a few species, or cylindrical with a lateral flattening in others; in most species, they are auriculate with a lateral groove. The eyes are prominent behind the rhinophores on the sides of the neck. The head and neck are usually offset from the body at the level of the parapodia by a pair of lateral furrows. These may be joined ventrally across the foot by a shallow groove which separates the short 'ancestral' sole from the posterior or visceral foot.

Crawling is achieved by the short anterior sole only in some species (T. Gascoigne personal communication; R. Burn personal observation), but by the whole foot in most species. One small Lizard Island species has only the anterior sole and carries the visceral mass clear of the substratum and the parapodia spread widely at all times (R. Burn personal observation). The anterior edge of the foot is rounded, sometimes expanded to angular corners, rarely to tentaculiform corners. The anus and female aperture open into the right lateral furrow, the penis lies in its sac beneath the right rhinophore. Behind the head rises the pericardium, from which a number of dorsal hepatic vessels branch and divide distally. The branching pattern of these vessels is a valuable taxonomic character (Marcus, Ev. 1980, 1982).

The parapodia vary considerably. In *Elysiella*, they are low and thick, and proximal to the tail. They are frilled in the Central American genera *Tridachia* and *Tridachiella*, in the latter excessively so. The margins may be smooth, papillose, or lobed, rarely with dendritic papillae which project upwards. The margins

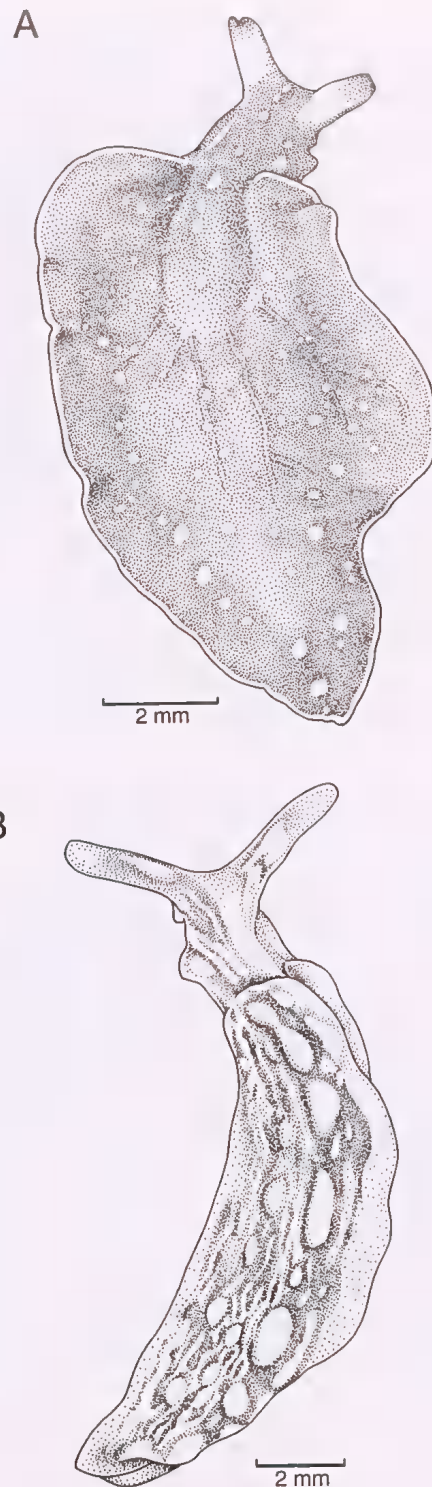


Figure 16.48 Family Elysiidae. A, *Elysia* sp., with parapodia widespread. B, *Thuridilla* sp., with parapodia folded together over dorsum. (A, B, after photographs by N. Coleman) [R. Plant]

may meet evenly, or they may form siphonal openings or chimneys in two, three or more places. More often than not, the parapodia reach right to the tail, and in *Tridachia* only are joined anteriorly across the neck. The parapodia are not used for swimming.

Generally the pharynx lacks a crop and oesophageal diverticulum, but one or the other or both may be present. The radular teeth are variable in shape; but are generally pointed and denticulate along one, two or three cutting edges. In *Thuridilla*, they are short and broad, and coarsely denticulate laterally. The few species of *Elysia* that feed on *Acetabularia* and *Polyphysa* have very long curved teeth. Those that feed on diatoms and *Zostera* have very short, sharply angled teeth. The nerve ring has three small ganglia on the very short visceral loop.

The reproductive organs have been well studied in a small number of species; quite a few differences have been revealed. The penis is only exceptionally armed with a cuticular stylet. The prostate gland branches are spread throughout the visceral mass, and rarely a seminal vesicle is attached to the vas deferens. One female aperture is far more common than two. There may be a globular bursa copulatrix with short or long vaginal duct entering the lower oviduct, or the bursa may be attached to the inner end of the oviduct at or close to the division of the spermiduct and, rarely, a seminal receptacle may be close by. If the bursa is attached to the inner oviduct, it may have a separate vaginal duct opening dorsally beside the pericardium. In the southern Western Australian *Elysia filicauda*, one of a pair of bursae just beneath the dorsal epithelium behind the pericardium forms a vaginal pore at copulation for the reception of sperm (Jensen & Wells 1990). This species also has a genital receptacle rising from the mucous gland. Similarly disposed pairs of bursae are reported in other species but are not known to open externally. Copulation is usually reciprocal in elysiids; it may even involve more than two individuals as in the Florida *Elysia patina* (Jensen 1986). In *Elysia maoria* from New Zealand and south-eastern Australia, copulation can be reciprocal with the animals broadside on: the penis of each is plunged through the epithelial tissue of the posterior right parapodium of the other, and vice versa. Or it can be non-reciprocal, one animal approaching the other and plunging its penis into any part of the body (Reid 1964; R. Burn personal observation).

Australia has a rich elysioid fauna, but relatively few species have been recorded (Allan 1950; Thompson 1973b; Burn 1989; Jensen & Wells 1990). Along southern temperate shores, the small *Elysia coodgensis* is particularly common in shallow intertidal rock pools and subtidal sand flats where it exploits a range of filamentous green algae (Jensen 1991). For many years, *E. coodgensis* has been confused with, and identified as, *E. australis*, which originally was collected in Sydney Harbour (Quoy & Gaimard 1832). Both species grow to 25 mm in length, but *E. australis* is broader with long thin whip-like rhinophores. It lives on intertidal sand flats in protected bays and estuaries from central to southern New South Wales, and burrows down into the surface film of the substratum during low tide. *Elysia australis* may be identical with *E. chilensis* from India and Hong Kong (Jensen 1985), another species with whip-like rhinophores.

Elysia maoria matches exactly the dark green colour of *Codium*, on which it is found in New South Wales and Victoria (Thompson 1973b; R. Burn personal observation). *Elysia furvacauda*, common on *Zostera* and *Heterozostera* from Westernport, Victoria to western South Australia (Burn 1990, personal observation), may be identical with *E. japonica* from Japan and Hong Kong (Jensen 1985).

In southern Western Australia, *E. filicauda* is pale greyish green with darker tips to the rhinophores, the very long and slender tail and parapodial chimneys. It feeds upon the green siphonaeal *Polyphysa peniculus* (Jensen & Wells 1990; Jensen 1991). *Elysia leucolegnote* is a big dark green species with white margin, which usually holds its parapodia open so that the shape of the animal resembles a mangrove leaf (Jensen 1990a). It can be found in the mangroves along the tidal creeks of Moreton Bay, southern Queensland (R. Burn personal observation). The widely distributed Indo-Pacific species, *E. ornata*, is recorded from northern New South Wales and Queensland (Allan 1950; Thompson 1973b). It is readily identified by the pale green body, black margined parapodia, and narrow white and broad orange bands along the parapodia. The lettuce-green *E. bennetti* has a wide northern distribution (Thompson 1973b; Carlson & Hoff 1978); white patches mottle the body, the parapodial edge is bright red or red-purple, and the inner edge of the parapodia may be bright orange.

Elysiella pusilla with its *Halimeda*-colouration, wide foot and short thick parapodia has a wide northern and Western Australian distribution (Jensen & Wells 1990; R. Burn personal observation), and is known under various synonyms from the wider Indo-Pacific.

The transverse parapodial lamellae of *Pattyclaya brycei*, from southern Western Australia (Jensen & Wells 1990) and possibly South Australia, sets it apart from other Australian elysiids. Its relatively smooth body and smooth radular teeth separates it from its only congener, the densely papillose *P. arena* from Guam, which has denticulate radular teeth (Carlson & Hoff 1977).

The 'blue-group' elysiids belong to the genus *Thuridilla*. These have short, triangular radular teeth with coarse lateral denticles, and the body is often deep blue or almost black in colour, ornamented with red, yellow, green and light blue stripes, bands and spots. *Thuridilla caerulea*, *T. bayeri*, *T. ratna*, *Thuridilla splendens*, and *T. gracilis* are all common species in Great Barrier Reef waters and elsewhere through the Indo-Pacific.

The Elysiidae of New Caledonia, Japan, Guam and southern Africa have been illustrated by Risbec (1928), Baba (1949, 1955, 1957, 1960), Carlson & Hoff (1978), and Gosliner (1987a), and Jensen (1985, 1990a) added to the Hong Kong fauna. Elysiids are eagerly devoured by *Gymnodoris* species (Kay & Young 1969; R. Burn personal observation), and their own feeding and learning behaviour has been studied (Jensen 1989, 1990a, 1990b). A parasitic copepod, *Splanchnotrophus elysiae*, has been described from *E. coodgensis* from southern Western Australia (Jensen 1990c).

Aspects of elysioid biology published in recent years include: chloroplast symbiosis or functional kleptoplasty; nutritional aspects of development and different developmental patterns; chlorophyll levels and temperature effects on production of metabolites; seasonal food changes, feeding methods and diets, variability of teeth numbers, food and habitat requirements, and diet (Kawaguti & Yamasu 1965; Taylor 1968; Clark, Busacca & Stirts 1979; Jensen 1980; Stirts & Clark 1980; Jensen & Clark 1983; Brandley 1984; West, Harrigan & Piece 1984; Gibson, Toews & Bleakney 1986; Raymond & Bleakney 1987; Waugh & Clark 1986; Clark *et al.* 1990).

Family Boselliidae

Boselliids are unusual, small sacoglossans (Fig. 16.49), generally less than 10 mm long, but may reach 17 mm. The family is presently not known from Australian waters. Four species occur in the Mediterranean and tropical west Atlantic, one species in the Red Sea (Marcus, Ev. 1978) and another in Hawaii (J.S. Bleakney personal communication). They live exclusively upon *Halimeda*, and their external appearance is very similar to that of a segment of the algae (Jensen 1980). The chromosome number of boselliids ($n = 7$, $2n = 14$; Mancino & Sordi 1964) also distinguishes them from all other sacoglossans. Foot structure, food and feeding, and reproduction and development are described by Clark (1984), Clark & Jensen (1981), Jensen (1980, 1981b), Ev. Marcus (1973, 1978) and Schmekel & Portmann (1982).

Boselliids could be confused with the elysioid *Elysiella pusilla* which occurs along the northern and western coastline of Australia (Jensen & Wells 1990; R. Burn personal observation) and lives on *Halimeda* which it mimics exactly in colour. *Elysiella pusilla* has low thick parapodia, even in small specimens, which separate it from Boselliidae.

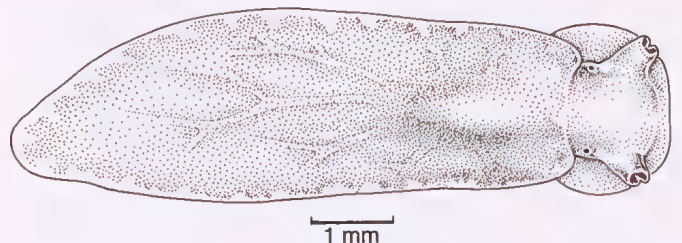


Figure 16.49 Family Boselliidae. *Bosellia mimetica*, dorsal view. [R. Plant]

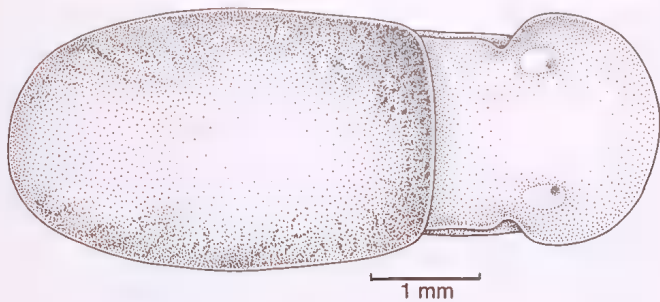


Figure 16.50 Family Gascoignellidae. *Gascoignella aprica*, dorsal view. (After Jensen 1985) [R. Plant]

Family Gascoignellidae

This monotypic family was created for an inconspicuous sacoglossan discovered on the mud-flats of Hong Kong (Jensen 1985). When similar habitats are explored in other places throughout the Indo-Pacific, it will probably be found to have a much wider distribution.

Gascoignella aprica is a small, broad animal not more than 8 mm long (Fig. 16.50). The body is flat, without rhinophores, or parapodia. The head is offset from the visceral mass by a distinct groove. The foot is very short. The anus and female aperture open into the groove on the right side. The penis with stylet lies in its sac below and behind the right eye. The circumoesophageal nerve ring encircles the oesophagus immediately behind the pharynx. The cerebral ganglia are not separate from the pedal ganglia. A subintestinal ganglion is present but nearly fused to the visceral ganglion on the very short triganglionate visceral loop.

Gascoignella aprica lives intertidally on mats of filamentous green algae, predominantly *Chaetomorpha* (Jensen 1985), where it is found crawling out in open sunlight. A sausage-shaped egg mass belonging to this species contained 590 eggs, in capsules measuring 100 x 90 µm.

Like *Platyhedyle*, *Gascoignella* is an aberrant, primitive elysioid adapted to an epiphytic life style. The laterally branching digestive glands with apical lobes are possibly precursors of the lateral lamellae of *Patylclaya*. *Gascoignella* needs to be revised, using cladistic methodology, to elucidate its relationships.

Family Platyhedylidae

This family contains only one small 4.5 mm long planarian-like opisthobranch from the western Mediterranean coasts of Italy and France (Fig. 16.51). When first described, *Platyhedyle denudata* was considered to be an acochlidean (Salvini-Plawen 1973). Later studies have shown that it belongs in the order Sacoglossa (Wawra 1979, 1988, 1991).

The body is flattened, elongate and slender, with the short foot separated from the long visceral mass by a shallow transverse groove, into which the female aperture and anus open on the right side. There are no rhinophores, parapodia, or cerata. The body is transparent, the eyes are visible in the head, and the paired digestive glands in the visceral mass are olive-green in colour. The circumoesophageal nerve ring lies behind the pharynx, and is typically elysioid in arrangement, with three ganglia along the slightly drawn-out visceral loop. A penis with stylet is held in a sac on the right side of the neck below and behind the right eye. The large bursa copulatrix stands at the inner end of the strong vagina which opens off the large oviduct close to the female aperture.

Platyhedyle, not unlike the tidal mud-flat species *Gascoignella aprica* from Hong Kong (Jensen 1985), inhabits the same biotope as acochlideans. It lives among coarse shell-sand at 3–4 m depth (Poizat 1978). As this habitat is still unexplored throughout most of the world, and particularly in Australia, the true distribution of *Platyhedyle* remains unknown.

Superfamily LIMAPONTIOIDEA

The members of this shell-less superfamily (= Stiligerioidea) are characterised by having aeolidiform cerata along each side of the body. The cerata may be large and leaf-like, or fusiform or stick-like, and generally contain a branch of the digestive gland. In many species ducts of the albumen gland also enter the cerata. The cerata may be numerous or sparse, and in some species there is a tendency for them to be grouped towards the posterior part of the body, or to be absent. The rhinophores vary from large bifid auriculate tentacles to simple tapering or cylindrical horns, and these may be further reduced to stumps, ridges, or be completely lost. The foot is usually a single sole, but *Cyerce* retains the transversely divided 'ancestral' anterior sole and posterior visceral sole. The anus may be antero-dorsal, right lateral, right mid-dorsal, or sub-terminal. The eyes may be contiguous between the rhinophores, but generally they are further apart and behind the rhinophores. The penis is generally armed with an apical stylet, and insemination may be hypodermic or vaginal. There may be one, two, or even three female apertures.

Limapontioideans generally feed on green algae. Three species are specialised feeders upon opisthobranch eggs, and a few others on rhodophyte (red) and phaeophyte (brown) algae. One species feeds on diatoms. The most recent works by the Danish sacoglossan specialist K.R. Jensen (personal communication) combine the limapontioidean families Costasiellidae, Hermaeidae and Limapontiidae, the last name having priority.

Family Caliphyllidae

This family (= Polybranchidae) comprises those aeolidiform sacoglossans (Fig. 16.52) with broad or flat leaf-like cerata which do not contain branches of the albumen gland. Exceptionally, the cerata are reduced to a few stick-like structures along the back. Five genera with 20 species between them have been referred to the family. Other species await description. Two genera, *Cyerce* and *Polybranchia*, are well-known members of Australia's tropical molluscan fauna. Anatomical descriptions have been published for *Caliphylla* (Marcus, Er. 1958a; Gascoigne 1979a; Schmekel & Portmann 1982), *Mourgona* (Marcus, Er. & Marcus, Ev. 1970), *Sohgenia* (Hamatani 1991) and *Cyerce* and *Polybranchia* by Bergh (1871) and Er. Marcus & Ev. Marcus (1970).

Caliphyllids are generally large animals, ranging up to 70 mm in length, although some are fully grown at 5 mm (Fig. 16.52A, B). The broad body is usually as wide as the foot, rounded in front and drawn out behind into a blunt point. The rhinophores are bifid for at least half the length in most species, or even to the base; in some species they are divided for only a short part of their length. Generally the rhinophores are auriculate, but in *Sohgenia* the groove is reduced almost to a line along the lateral side of the rhinophores. All genera except *Sohgenia* have rounded or pointed oral tentacles, hollowed below. The foot is broad with a rounded, or laterally angular, anterior edge. In *Cyerce*, the sole is divided at

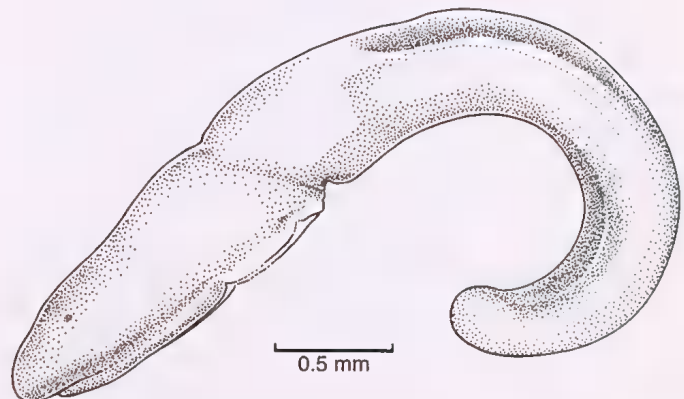


Figure 16.51 Family Platyhedylidae. *Platyhedyle denudata*, lateral view. (After Arnaud, Poizat & Salvini-Plawen 1986) [R. Plant]

16. OPISTHOBRANCHIA

the anterior third by a transverse groove; in other genera it is undivided. The eyes are visible behind the base of the rhinophores. The pericardium is a low, elongate prominence behind the head. In *Cyerce* and *Sohgenia*, the anus opens on a papilla to the right of the centre line mid-way between the eyes and pericardium. In the other genera, it opens in a right lateral position below or between the lowest cerata. The two or three reproductive apertures open on the right side below and behind the rhinophore.

The cerata are flat and leaf-like in *Caliphylla* and *Mourgona*. In *Cyerce*, they are flat and leaf-like (Fig. 16.52B), wedge-shaped, or thickened and cushion-like (Fig. 16.52A), and have a stout petiole and saucer-like end in *Polybranchia*, and are stick-like with an apical knob in *Sohgenia*. The digestive gland is absent from the cerata of *Sohgenia*; it just enters the stem in *Cyerce*, and enters and branches, sometimes extensively, in the cerata of the other genera. The edges of the cerata may be smooth, or beset with defensive and adhesive glandular swellings opening to the outside. Small conical papillae may be present on one or both faces of the cerata, and on the rhinophores, tentacles, head and pericardium. There are no albumen gland branches in the cerata.

The pharynx may have a small or large posterior ventral crop with a double lumen, or it may be excessively long (*Polybranchia*). An oesophageal diverticulum is absent in *Mourgona* and unknown in *Sohgenia*. The radular teeth are pointed and smooth in *Caliphylla* and short and laterally denticulate in *Polybranchia* and one species of *Mourgona*. In another species of *Mourgona*, and in *Cyerce*, they are very long and coarsely denticulate laterally and irregularly. Those of *Sohgenia* are finely pointed and coarsely denticulate laterally. The nerve ring encircles the oesophagus behind the pharynx, and the very short visceral loop is triganglionic, except in *Polybranchia* in which only the supra-intestinal and visceral ganglia are found.

Except for the nature of the penial tips, the reproductive organs of *Mourgona* and *Sohgenia* are not known. In other genera, the winding ampulla leads on as a short spermoviduct before it divides to male and female branches and receives the duct from the albumen gland. The female branch opens initially to the mucous gland. The bursa copulatrix is generally attached to the lower oviduct, but at least one species of *Cyerce* has a separate vaginal duct with its own external opening (Sanders-Esser 1980, 1984). The seminal receptacle lies nearer the inner end of the oviduct, and may be single or multiple. Usually the inner oviduct loops back on itself, forming a fertilisation chamber, and there may be a further loop connecting the seminal receptacle to the lower spermoviduct. A bilobed or elongate prostate gland enters the vas deferens distally. The penis has a long flagellum with apical stylet in *Caliphylla*, an apical stylet in *Mourgona*, and a long straight or short hooked stylet in *Cyerce*. In *Polybranchia*, the penis is long and tapering and may have a stylet, though in two species it is beset with spiny papillae. In *Sohgenia*, there is no stylet.

Generally caliphyllids are dull coloured animals showing only the light to dark greenish digestive gland of the body and cerata. However, some species of *Cyerce* are spectacularly coloured. The Mediterranean and tropical west Atlantic *C. cristallina* has conspicuous white patches on the body, rhinophores and cerata, overlaid with smaller bright red patches. The Indo-Pacific *C. elegans* is translucent yellowish with golden yellow edgings to the cerata, *C. nigricans* and *C. nigra* are both black with orange spots and/or white bars on one or both sides of the cerata, and *C. kikutarobabai* has inflated brown cerata with white spots.

According to the available data on food, *Caliphylla* is restricted to *Bryopsis*, *Cyerce* to *Penicillus*, *Halimeda*, *Chlorodesmis* and *Cladophora*, *Polybranchia* to *Caulerpa* and *Valonia*, and *Sohgenia* to *Halimeda* and *Udotea*. *Mourgona* secretes a toxic, viscid mucus and autotomises cerata when physically disturbed, the toxin apparently originating from its food alga *Cymopolia* (Jensen 1984). Diets and feeding methods of *Cyerce* and *Mourgona* have been reviewed (Jensen 1980, 1981b), and their alimentary systems compared with those of *Caliphylla* (Jensen 1991).

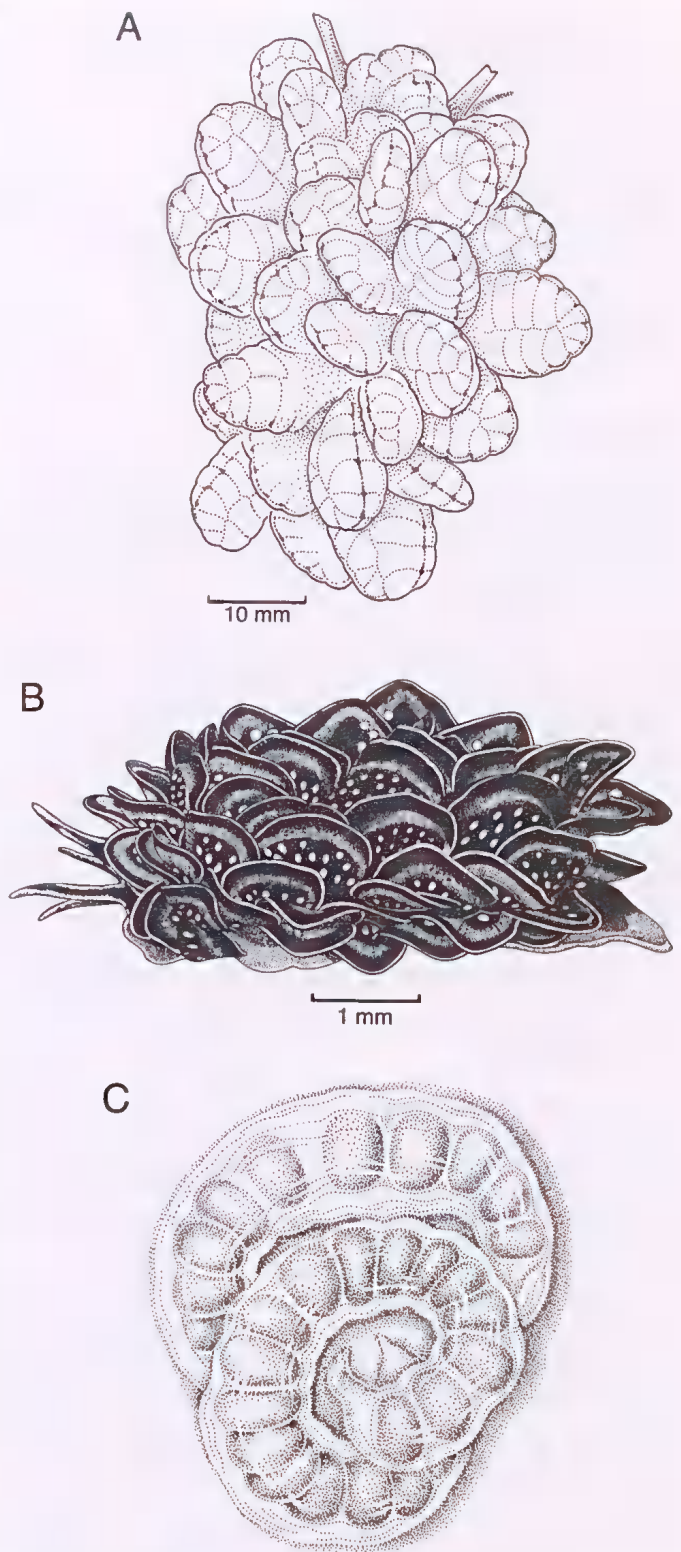


Figure 16.52 Family Caliphyllidae. A, *Cyerce elegans*, dorsal view. B, *Cyerce nigra*, dorsal view. C, egg mass of *Polybranchia pallens*. (A, after photograph by I. Loch) [A, C, R. Plant; B, T.E. Thompson]

Caliphyllids generally lay flat, spiral bands of minute eggs from which planktotrophic veligers emerge. The Mediterranean and tropical west Atlantic *Cyerce antillensis* lays larger eggs which develop to lecithotrophic veligers (Clark & Jensen 1981). In Hawaii, *Polybranchia* species are reported to lay a three whorled cylindrical gelatinous coil (Kay 1979). In southern Australia, *P. pallens* lays a 6 mm diameter cylindrical coil of 12 to 35 very large eggs in an irregular two whorled coil 25–35 mm across on the underside of stones or shells (Fig. 16.52C). From these eggs emerge bright pink, 4–5 mm long, crawling young with fully developed rhinophores and cerata (Burn 1989, personal observation).

The Caliphyllidae known from Australian seas belong to only two genera, *Cyerce* and *Polybranchia*. The temperate *P. pallens* and the tropical *P. orientale* (Baba & Hamatani 1971) are very similar, but differ markedly in their habits and developmental patterns. Both shed cerata at the slightest provocation. *Polybranchia pallens* often associates with *Caulerpa longifolia*, and *P. orientale* is found in association with *C. racemosa* or lying motionless on the substratum, apparently absorbing sunlight. *Cyerce* species are found along the tropical northern coasts, from northern New South Wales to North West Cape, Western Australia. *Cyerce nigricans* is the best-known species and is often featured in books, articles and documentary films on the Great Barrier Reef. It is black with orange spots on both sides of the cerata. *Cyerce nigra* is also black but has spots only on the dorsal face of the cerata, and white transverse strips on the other side (Fig. 16.52B). This species occurs on the west coast of Western Australia as well as Queensland (R. Burn personal observation). *Cyerce elegans* (Fig. 16.52A), from the Great Barrier Reef, is transparent yellowish in colour with inflated cerata margined with a line of golden scallops or indentations, their faces marked by a slender dendritic tracery of yellowish white. Also from the Great Barrier Reef is *C. kikutarobabai*, a small species with white spotted brown cerata. Other caliphyllid-like species from tropical waters await description and identification.

Family Costasiellidae

A small family of one genus and 12 named species, characterised by large contiguous eyes lying between the rhinophores, instead of behind them (Fig. 16.53). The named species are from the Mediterranean, the tropical West Atlantic, Japan, Hong Kong and the western Pacific. At least six Australian species await description or identification; two of these are tropical and two are temperate.

Apart from the distinctive eyes, most costasiellids can be distinguished by a broad, thick ridge from each rhinophoral base to the anterior edge of the head beside the mouth (Fig. 16.53). The mouth thus lies in a deep furrow between the two ridges. In some species, the ridges are obsolete or even absent (R. Burn personal observation). The living animals rarely exceed 10 mm in length. The body is generally broad anteriorly, and tapers to a blunt tail. The foot may be rounded in front, or may have distinctly tentaculiform corners. The posterior foot may be divided by a transverse groove and contain digestive diverticula; if so it closely resembles, and possibly functions as, a large horizontal ceras (Marcus, Ev. & Marcus, Er. 1969b; Clark 1984; R. Burn personal observation). The rhinophores are usually long and gently tapering, and generally have a lateral groove at the base. The cerata are broadly fusiform, with blunt tips. Each contains a knobbed branch of the digestive gland, around which slender branches of the albumen gland wind. The cerata lie over one another in life, but, as they arise from the body more laterally than dorsally, there is a wide space dorsally. The pericardium is large and prominent, wider and higher in front, and drawn out behind in a narrower and lower renal ridge. The pericardium is rounded above, but in one of the undescribed temperate Australian species it is dorsally concave, with spreading edges wider than the pericardial outline on the body. The anus (on a low papilla) and the renal pore open on the anterior right side of the pericardium, and a melanin gland is generally visible close by. The two or three reproductive apertures open close together below and behind the right rhinophore. Exceptionally, there is a fourth reproductive aperture, a left lateral pore from the vesicle for excess seminal fluids (Marcus, Ev. & Marcus, Er. 1969b).

The pharynx is small and generally lacks a crop. There is usually no oesophageal diverticulum. The radular teeth are blade-like and non-denticulate. The nerve ring lies behind the pharynx and the short visceral loop is triganglionate. The penis is long and carrot-shaped, rarely distally swollen and mace-like (R. Burn personal observation). A minute cuticular stylet is present in one species. The vas deferens has a bilobed or multilobed prostate gland near its point of origin. The vagina may open off the fundus

of the penial atrium, or it may have a separate aperture beyond the oviduct. At its inner end, the vagina opens to a large fertilisation chamber, which in turn connects by a long duct to the bursa copulatrix or the excess seminal fluid vesicle on the left side. The ampulla is winding or convoluted, and the spermoviduct is short.

Costasiellids are generally whitish but appear dark green as a result of the contents of the digestive gland, and often have much black pigment over all surfaces except the sole. A broad white band may traverse the neck and surround the eyes, and one species has a conspicuous green-blue iridescent 'eye-spot' or iridophore between the eyes and pericardium. An undescribed species from Lizard Island, northern Queensland, has a white body with black median stripe and rhinophoral tips, pink-tipped cerata and bright green digestive glands (R. Burn personal observation).

Two tropical western Atlantic species feed on the green alga *Avrainvillea nigricans*. *Costasiella ocellifera* crawls and lives on the surface of the alga, and *C. nonotai* burrows in to feed and deposit egg masses (Clark 1984). A dark green *Costasiella* species lives on algae of this genus at Lizard Island, Queensland (R. Burn personal observation). The Japanese *C. formicarius* is found on green algae in the intertidal zone (Baba 1959a), and in Hong Kong, *C. pallida* occurs on small patches of the filamentous green alga *Vaucheria vipera* in the high intertidal of a sandbar near mangroves (Jensen 1990a). Two undescribed south-eastern Australian species are found on patches of short green alga growing on intertidal and subtidal sand flats (R. Burn personal observation). Another Lizard Island species, without ridges on the head, was found at 20 m on *Halimeda macrolobata* (R.C. Willan personal communication). This last species is possibly identical with *C. illa* from the Caroline Islands, Micronesia (Marcus, Er. 1965).

Little is known about the ecology or life history of costasiellids. The egg masses are small spiral cords of three and a half whorls containing double rows of eggs which are laid on *Halimeda* (R.C. Willan personal communication), or sausage-shaped and containing 200 to 800 eggs in capsules 130 x 100 µm in size

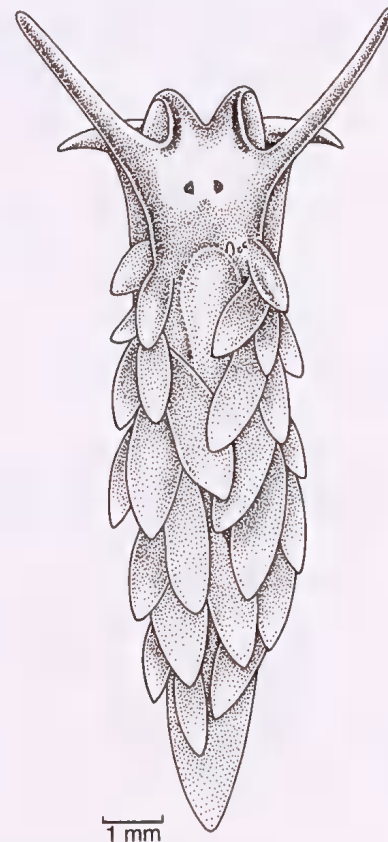


Figure 16.53 Family Costasiellidae. *Costasiella* sp. from south-eastern Australia, dorsal view. (After sketch by R. Burn) [R. Plant]

(Jensen 1990a). The tropical west Atlantic *C. ocellifera* lays 75 large eggs almost 100 μm in diameter from which crawling young emerge; *C. nonotai* lays smaller eggs which develop to lecithotrophic or short term veligers (Clark & Jensen 1981). The kleptoplasty of *C. ocellifera* has been studied in detail and is one of the best examples of this phenomenon (Clark, Jensen, Stirts & Fermin 1981). The dietary constraints and feeding methods of *C. ocellifera*, and the feeding behaviour of *C. pallida* have also been studied (Jensen 1980, 1981b, 1990a).

Family Hermaeidae

At present, this cosmopolitan family contains only two genera, *Hermaea* (Fig. 16.54) and *Aplysiopsis*, and 14 species. Although only one species has been reported formally from Australia, both genera are present and are well represented at species level. Good reviews of the genera, their anatomy and biology are to be found in Er. Marcus (1955), Gonor (1961b), Ev. Marcus & Er. Marcus (1967a), Gascoigne (1979b) and Clark (1982b). The genera appear to need division.

Hermaeids are stout or slender aeolidiform sacoglossans ranging in length from 5–35 mm, though most are less than 20 mm. The rhinophores are auriculate, flared and curiously stepped at the tips; they are expanded to form a basal lobe in some species, and often droop somewhat distally. The eyes are behind the rhinophores. A pair of angular oral lobes project laterally above the mouth. The pericardium lies behind the neck, and the anus is either on a long posteriorly directed papilla or flush with the neck and opens immediately in front in the mid-line. The male reproductive aperture is on the right side behind and below the rhinophore, and a short distance anterior to the female aperture. The foot is wide in *Aplysiopsis*, and very slender and long in *Hermaea*, in which the anterior edge is rounded or laterally angulate. The cerata may vary from stoutly fusiform, to sometimes a little flattened in *Aplysiopsis*. Often a branching pattern of ribs is visible on the inner side of each ceras. In *Hermaea*, the cerata are either elongate and paddle-shaped (Fig. 16.54), the digestive gland within branching in the one plane, or elongate and fusiform, with angular knobs corresponding to the branches of the digestive gland. Many *Hermaea* have only a single row of cerata, alternately large and small, along each side of the body. There are no ducts of the albumen gland in the cerata.

The pharynx is small in *Hermaea*, and larger in *Aplysiopsis* with a big, projecting, ventral radular ascus. There is no pharyngeal crop. An oesophageal diverticulum is generally present, and may be small or elongate. In *Hermaea*, it is often visible in the left side of the neck due to the brightly coloured food contents. The radular teeth take one of two forms. Those in *Hermaea* are short with rather blunt, usually laterally denticulate cusps. In *Aplysiopsis*, they are longer and sabot-shaped, with a bluntly rounded tip, a pair of denticulate laminae on the cutting face, and a median keel on the dorsal side. The circumoesophageal nerve ring encircles the oesophagus behind the pharynx, and the visceral loop is very short and passes through two or three ganglia.

The reproductive system has only a single female aperture in all species. In *Hermaea*, the plan of the ducts and glands is very uniform; the winding ampulla leads to a short spermiduct which divides into male and female branches. The female branch, the inner oviduct, receives the separate ducts of the large globular bursa copulatrix, the smaller seminal receptacle, and the albumen gland, then enters the capsule gland to emerge as the oviduct, opening through the female aperture. Near its point of origin, the vas deferens receives the contents of the prostate gland. The cylindrical penis is unarmed and may have a seminal reservoir in its swollen base. At least one species in *Aplysiopsis* has the same reproductive plan as *Hermaea* with two seminal vesicles, except that the inner oviduct loops back on itself to form a fertilisation chamber (K. Baba personal communication).

In other species, the bursa copulatrix is attached by a vaginal duct most often to the lower oviduct, and a second inner efferent duct links the bursa copulatrix to the inner oviduct near its division from

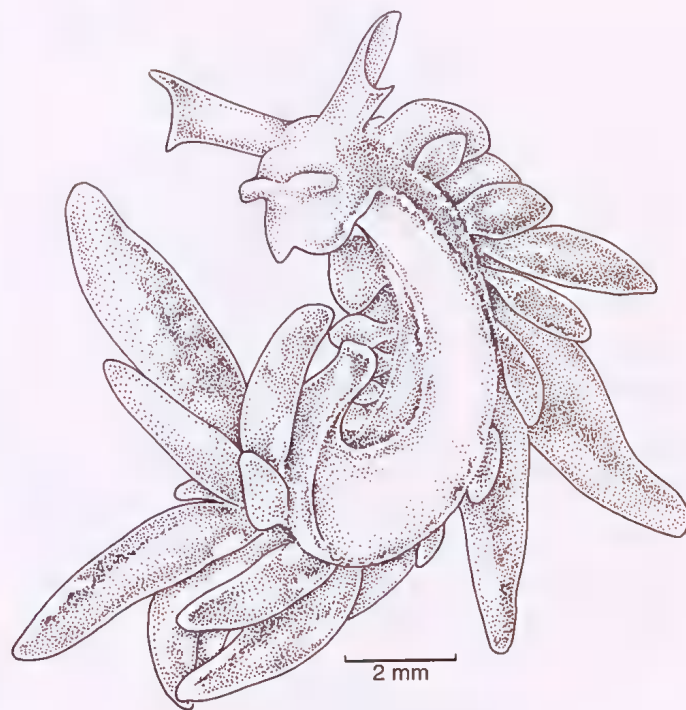


Figure 16.54 Family Hermaeidae. *Hermaea* sp., ventral view. (After photograph by I. Kirwen) [R. Plant]

the spermiduct. The inner oviduct then enters a fertilisation chamber or capsule gland before winding away as the large oviduct, to join with the mucous gland and open through the female aperture (Gonor 1961b; Schmekel & Portmann 1982; K. Baba personal communication). The vas deferens receives the duct of the prostate gland close to the division from the spermiduct. The penis may be a simple, long or short cylindrical papilla, or a short and conical papilla with or without a cuticular stylet, or a slender barb-shaped papilla (Gonor 1961b; K. Baba personal communication).

Hermaeids may be virtually colourless (*Hermaea*) or heavily pigmented (*Aplysiopsis*). *Hermaea* usually has a transparent body, sometimes overlaid with a peppering of minute red or black spots, through which the pinkish muscular pharynx and coloured oesophageal diverticulum, digestive glands and ducts are easily seen. The very brightly coloured Mediterranean and western European *H. variopicta* is purple, orange and white on the body, with yellow lines on the cerata. *Aplysiopsis* may be entirely black or green, but some species have brown or yellowish patterns on the head rhinophores and body, and longitudinal stripes along the cerata (Baba 1949; Schmekel & Portmann 1982).

Some species of *Hermaea* feed upon the red alga *Griffithsia*, and at times the ruby-red colouration of their digestive glands in the cerata is almost fluorescent. Other species have brown or green digestive glands, suggesting that the genus has a far greater range of foods than the one rhodophyte genus. *Aplysiopsis* feeds on *Rhizoclonium*, *Urospora* and *Chaetomorpha* in California (Gonor 1961b) and on *Cladophora* in Florida (Clark 1982b) and Japan (Baba 1959a). *Aplysiopsis* lays a string of as many as 4500 eggs 71 μm in diameter wound around the alga, or a flat ribbon about 20 eggs wide, which develop to planktotrophic veligers. The genus *Hermaea* has planktotrophic development. The European *H. bifida* lays a thick winding or spiral coil of up to 550 eggs 48–54 μm diameter in capsules three times as long and twice as wide. The western Atlantic *H. cruciata* lays slightly larger eggs, 77 μm in diameter. A small, 6 mm long, temperate Australian *Hermaea* with pale green digestive glands deposits ovoid egg masses about 2 x 1 mm in size on the lower stems of its food alga. Sand grains adhere to the sticky surface of the mass as soon as it is laid. The white eggs are about 70 μm in diameter in capsules 120 x 100 μm , and development appears to be planktotrophic (R. Burn personal observation).

Mating in this last-mentioned species is fleeting – between 10 and 15 seconds – as the animals pause side-by-side in passing. Each animal merely touches the tip of the everted long unarmed penis on the female aperture of the other, and, by rapidly moving its penial tip from side to side, discharges a zigzag of cream sperm in a pad over the area of the female opening. The latter enlarges to reveal a bell-shaped cavity which engorges and closes over the sperm pad, which can be seen as an opaque mass moving along the vaginal duct within the body until lost from view, evidently at the point of entry to the bursa copulatrix (R. Burn personal observation).

The genus *Hermaea* appears to belong to the southern or temperate molluscan fauna of Australia. One species, *H. evelinmarcusae*, has a wide distribution from Rottnest Island, Western Australia to Botany Bay, New South Wales (Jensen 1993a; R. Burn personal observation). Four undescribed species have been reported from Westernport, Victoria (Burn 1990). The species are distinguished by the shape of the cerata, the colour of the digestive gland, the presence or absence of a high anal papilla, and the presence or absence of a dark stripe on the dorsal side of the pharynx. *Aplysiopsis formosa* of the North Atlantic and Mediterranean (Ortea, Bacallado & Pérez Sánchez 1990) where it feeds on *Cladophora prolifera*, has been discovered on the central Victorian coastline associated with the same alga (R. Burn personal observation). A small *Aplysiopsis* from New South Wales is yellowish with brown stripes on the head and cerata; it resembles *A. orientalis* from Japan (Baba 1949).

Family Limapontiidae

The family Limapontiidae (= Stiligeridae, Oleidae, Alderiidae) is by far the largest aeolidiform sacoglossan group, with seven or eight genera and more than 40 species. The species show a trend towards reduced rhinophores and fewer or no cerata (Fig. 16.55). The family may be conveniently divided into subfamilies according to the shape of the teeth: sabot-shaped in Limapontiinae, and awl-shaped in Stiligerinae. The few reports of the family from Australia mostly lack good descriptions or identifications (Burn 1972, 1974a, 1974b, 1974d, 1990; Thompson 1973b; Jensen 1993a), and there are as many as 10 species from various parts of the continent awaiting formal description.

In general, limapontiids are small sacoglossans less than 20 mm in length, though under exceptional circumstances such as an abundance of food, specimens 25–35 mm, and even up to 75 mm can be found. The body is generally slender, tapering to a blunt point behind. In some genera such as *Alderia*, *Alderopsis*, *Limapontia* and a few *Ercolania* (Fig. 16.55), the body is broader and flattened, with a correspondingly broader foot. The anterior edge of the foot is rounded; only rarely are there tentaculiform corners. In *Stiliger* and *Placida* the rhinophores are generally long and tapering, and bear a basal lateral groove, whereas in *Ercolania* and *Calliopaea* they are more cylindrical, sometimes flattened laterally. In *Alderia*, *Alderopsis*, *Olea*, *Limapontia* and some *Ercolania*, the rhinophores are reduced to short stumps or ridges, and may be absent altogether. The eyes are behind the rhinophores, usually in clear or whitish patches on the side of the neck. The pericardium is a low or raised hemispherical prominence on the dorsum well behind the eyes. In some *Ercolania* it extends rearwards as a narrower, long renal ridge to about the third quarter of the body length.

The anus in *Stiliger* species opens on a papilla on the front edge of the pericardium. In the other genera, it generally opens through a flat pore on the front right quarter of the pericardium, but there are notable exceptions. The anal aperture of *Limapontia* occurs on the right of the pericardium at or behind mid-length, and in *L. depressa* it is in the subterminal mid-line. That of *Ercolania felinus* from New Zealand, and *E. margaritae* from south-eastern Australia, is on a high papilla beside the right rear quarter of the pericardium. In an undescribed *Ercolania* from the latter region, the anus opens on a high papilla on the right side of the renal ridge at the posterior third.

The male aperture lies below and behind the right rhinophore, the one or two female apertures lie more posteriorly, generally below the foremost cerata. In some species a whitish raised vaginal ridge is present below the anterior cerata on the right side. This ridge indicates that the vaginal bursa lies just below the epithelium and that insemination is hypodermic.

The fusiform cerata vary from long and slender, particularly in fully adult specimens, to short and stout, and even globular with distinct petioles. They are lacking in *Limapontia*. The digestive gland may be simple, knobbed or distinctively branched within the cerata. Ducts of the albumen gland may extend into the cerata; their presence or absence has specific, rather than generic significance. The cerata are numerous in some species of *Stiliger* and *Ercolania*. They may form a single row along each side of the dorsum, as in *Alderopsis*, or occur only on the posterior half of the body, as in *Alderia* and *Olea*.

Many limapontiids are entirely black, though pigmentation differences have been noted between intertidal and subtidal populations of the same species (Burn 1974a; Jensen 1985). Other species are brownish, greenish or yellowish with lighter or darker digestive gland pigmentation. The cerata of a few species, particularly of *Stiliger*, are strikingly pigmented, with orange tips above a blue band, or long black tips above a bright deep orange lower part.

The pharynx bears a projecting ventral ascus but no pharyngeal crop. An oesophageal diverticulum may be present, and can vary considerably in length. The radular teeth are either sabot-shaped with a deep spoon-like cavity which fits over the basal keep of the next tooth, or awl-shaped with a sharp point. The teeth are not denticulate. *Olea* has only a vestigial radula. The

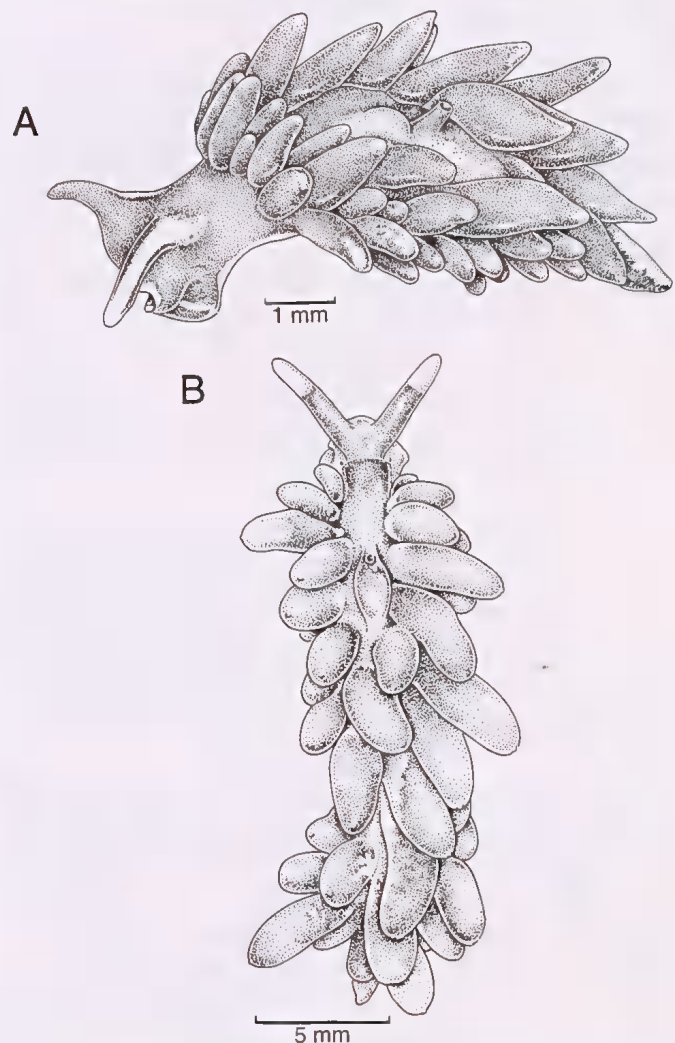


Figure 16.55 Family Limapontiidae. A, *Ercolania margaritae*, dorso-lateral view. B, *Stiliger smaragdinus*, dorsal view. (A, after photograph by R.C. Willan; B, after photograph by I. Kirwen) [R. Plant]

circumoesophageal nerve ring encircles the oesophagus behind the pharynx, and the very short visceral loop comprises only the visceral and supra-intestinal ganglia; the former is usually the larger. *Alderia* and one Mediterranean species of *Stiliger* lack the muscular ventricle and thin-walled auricle which make up the sacoglossan heart. Instead the entire pericardium pulsates slowly from the posterior end forwards (Gascoigne & Sordi 1980).

The reproductive organs have a long thick ampulla and short spermoviduct which divides to male and female branches. The vas deferens receives the duct of the often bilobed prostate gland close to the point of origin. The penis is armed with a stylet which may be short and hooked, long and curved (sometimes with minute hooks or lamellar plates along the inner side of the curve), or very long and tapering. The female branch receives the duct of the albumen gland, then with few exceptions, loops round on itself through a swollen fertilisation chamber. The spherical seminal or germinal receptacle, with its short duct, opens off the inner oviduct at or near this point. In *Alderia*, it enters higher up at the first part of the inner oviduct.

A vaginal duct enters the outer end of the fertilisation chamber (except in *Alderia*). The vaginal duct may open to the exterior, or enter a large bursa copulatrix pressed hard against the body wall which shows externally as a whitish vaginal ridge, rarely a cleft, below the anterior cerata. The open vagina and the subepithelial bursa function similarly, the first by receiving sperm directly from an inserted penis, the second by receiving sperm directly from a hypodermic injection by the penial stylet. In *Alderia*, copulation is by hypodermic injection, usually close to the somewhat dorsal seminal receptacle but can be to any part of the body. It is not known how the injected sperm make their way to the seminal receptacle in *Alderia*. The inner oviduct passes through the mucous gland to the large oviduct which opens closely behind the male or penial aperture.

Limapontiids lay small to large sausage-shaped or spirally coiled egg masses filled with immense numbers of minute eggs which develop planktotrophically, or exceptionally, very few large eggs from which crawling young emerge (Clark & Jensen 1981; Schmekel & Portmann 1982). Feeding and/or reproduction have been well studied by Gascoigne (1956), Chia (1971) and Crane (1971). Bleakney (1988, 1989, 1990) examined radular teeth and penial style variations between populations of *Alderia* and *Stiliger*, and Sanders-Esser (1980, 1984) studied the reproductive organs of the genera of the family. The nervous system of *Alderia* was described by Gascoigne (1974b). Jensen (1975a, 1975b, 1977, 1981b) and Usuki (1977) examined feeding methods, nutrition, salinity tolerance, and consumer potential of *Ercolania* and *Limapontia*. Chloroplast retention and photosynthetic function have been surveyed in species from Florida and New England with variable results (Clark *et al.* 1990).

Limapontiids eat a wide range of chlorophytic algae, and some species usually found on *Codium* will grow rapidly to a much larger size when transferred to another acceptable food alga. Beside *Codium*, limapontiids are known to feed on *Bryopsis*, *Cladophora*, *Dictyosphaeria*, *Vaucheria*, *Chaetomorpha*, *Valonia*, *Rhizoclonium* and *Polysiphona*. Two species of *Calliopaea*, and *Olea*, feed on the eggs of species in the opisthobranch genera *Philine*, *Retusa*, *Favorinus*, *Haminoea*, *Aglaja* and *Gastropteron* (Haefelfinger 1962; Crane 1971; Lemche 1974).

Small aeolidiform sacoglossans, tentatively placed in the genus *Ercolania*, eat the cytoplasm, and lay eggs within, the vesicles of *Valonia* and *Boergesenia* in Queensland and Western Australia (Loch 1989; R. Burn personal observation). How the animals enter and leave the vesicle, and how mating might take place when there is only one animal per vesicle are conjectural. *Alderia modesta* and *Limapontia depressa* both inhabit salt marsh areas with considerable exposure during low tide, and it is thought that the posterior anal position is adaptive for faecal removal during this time (Evans 1953). A number of limapontiids can tolerate reduced salinities of 15–20‰, even as low as 8.5‰ (Marcus, Ev. 1972c).

Limapontiids live in tropical and temperate waters around the world. A few species reach the latitudes of northern Europe and southern New Zealand. A number of species are reported for Australia seas. *Placida fralila* and the cosmopolitan *P. dendritica* are both dark green and are found on *Codium fragile* in southern Queensland and New South Wales (Burn 1966a; Thompson 1973b; Bleakney 1989). *Ercolania margaritae* (Fig. 16.55A) can be found feeding on filamentous green alga growing in mid-intertidal pools on rock platforms, or on *Bryopsis* in deeper water, in Victoria and Tasmania (Burn 1974a; Gascoigne 1976). Another black *Ercolania* occurs on the salt marshes surrounding Moreton Bay, southern Queensland, and has been incorrectly identified as the North American east coast *E. fuscata* (Thompson 1973b; Gascoigne 1978). Three other *Ercolania* species are known from Victorian shores, as yet undescribed, and one each from northern Queensland and southern Western Australia (Burn 1990, personal observation; Jensen 1993a; J.S. Bleakney personal communication). *Stiliger cremoniana*, known from the Mediterranean and Japan (Baba 1959a; Schmekel & Portmann 1982), has been found along the east coast from Lizard Island to southern New South Wales (R.C. Willan personal communication; R. Burn personal observation). It has an orange body, and orange cerata with long black tips. *Stiliger smaragdinus* (Fig. 16.55B) has a wide distribution in the western Pacific from Japan (Baba 1949), to the Marshall Islands (Johnson & Boucher 1983), New Zealand (R.C. Willan personal communication), and all round Australia (Burn 1972; Jensen 1993a, in press). In Victorian waters, this species attains 75 mm in length. Additional species of *Stiliger* and *Ercolania* have been described from southern Western Australia (Jensen 1993a). *Limapontia* has been found on one occasion in southern Australia and once in southern New Zealand (Burn 1974b, 1974d), but these records have not been confirmed by subsequent collection.

The genera *Alderia*, *Calliopaea*, *Alderiopsis* and *Olea* are not known from Australia.

Order ANASPIDEA

In general, anaspideans are large opisthobranchs in which the shell is retained merely as an internal plate over the gill and heart, or lost altogether. They are characterised by a head with two pairs of laterally grooved tentacles (in most taxa), flattened oral tentacles around the mouth, and erect cylindrical rhinophores dorsally. Individuals are hermaphroditic, and the genital tract has a ciliated groove along the right side of the body from the female gonopore to an eversible penis beneath the right oral tentacle. The plump body is embraced laterally by flap-like, projecting parapodia that represent upgrowths from the foot margins. Besides the plicate gill and heart, the mantle cavity also contains two novel glands, the opaline gland on the floor and the 'purple' gland on the roof. The former secretes a colourless repugnatory fluid, and the latter produces the well-known 'ink' of sea hares. The 'ink' is a deep violet-purple colour. Its major component, phycobilin, is manufactured by sea hares by breakdown and concentration of pigments ingested in the rhodophyte algae upon which the animals feed. Nolen *et al.* (1995) have demonstrated experimentally that the 'ink' serves to deter predators.

The name Anaspidea is also currently in use for a group of fossil agnathan fishes (for example, Archer & Clayton 1984), and hence some malacologists prefer to call this order Aplysiomorpha. However, Anaspidea is well entrenched for the opisthobranch order and it seems likely that this dual usage will continue unless the International Commission on Zoological Nomenclature establishes rules governing group names above the category of superfamily.

Two groups of anaspideans are recognised, the superfamilies Akerioidea and Aplysioidea, each comprising one family. Akerioidea are characterised by having an external, coiled shell, and a simple head shield, not elaborated into oral tentacles or rhinophores. In the Aplysioidea, the shell is either a vestigial plate roofing the mantle cavity or absent; oral tentacles and rhinophores are always present. Thompson & Seaward (1989) found that both groups exhibit unequal cleavage of the ovum (a rare character state in other opisthobranchs) and both share derived spermatological features.

Superfamily AKEROIDEA

Family Akeridae

Members of this very small family have an external, ovate, posteriorly flattened shell into which the animal cannot retract completely (Fig. 16.56). The small head shield is elongate and depressed, truncate in front, and tapered to a single lobe behind. There are no oral tentacles or rhinophores. The family is represented solely by four species in the genus *Akera* – *A. bicincta* and *A. soluta* in the Indo-West Pacific, and *A. bayeri* and *A. bullata* in the Atlantic Ocean. The last of these has been studied most extensively. Despite several thorough anatomical investigations (Guiart 1901; Vayssi re 1903; Perrier & Fischer 1911; Morton & Holme 1955; Marcus, Ev. & Marcus, Er. 1967a; Marcus, Ev. 1970; Morton 1972; Thompson & Seaward 1989), the placement of this family within the Anaspeidea was contested until quite recently (for example, Marcus, Ev. 1970, 1972d; Schmekel 1985) on the grounds that the nervous and reproductive systems are like those seen in the Cephalaspeidea.

The shell is fragile and more or less transparent, reaching 45 mm in length in Australian *Akera soluta*. The protoconch is sunken in the middle of the flattened spire. A thin periostracum covers the shell, and is raised into an upstanding flange at the keel. The body is almost twice the length of the shell and unable to retract completely. The margins of the foot are extended into large parapodia that normally fold over the head shield and shell. Guiart (1901) and Morton (1972) described the mantle cavity. The magnitude of the pallial caecum is noteworthy; it coils independently round the visceral spire and reaches the apex of the shell (Morton 1979). The mantle cavity contains a pair of broad, flat, strongly ciliated raphes and a transversely placed plicate gill. The gut of *Akera* shows derived features autapomorphic for Anaspeidea – the particular radular form and tooth shape, long tubular salivary glands, and a gizzard with cuticularised plates. The circumoesophageal nerve ring of six ganglia is located behind the pharynx. The visceral loop is long and somewhat tortored and the parietal and intestinal ganglia are separate and lie posteriorly. The prostate gland and vas deferens are in an open groove. The penial sheath bears a small cluster of cuticularised spines. The female gonopore has a leaf-like process. Copulation apparently occurs as in aplysiids, with two or more animals one behind the other in extended chains. The partner in front acts receives of sperm from the partner behind. Spawn consists of a long mucous string which is anchored in the substratum by one end and is deposited in a loose tangle. The eggs are minute, numerous and yellowish.

Akera soluta is recorded from all mainland Australian coasts. The second species, *A. bicincta*, is probably restricted to South Australia and southern Western Australia (Wells 1984; Burn 1989). *Akera* species live in a range of soft substrata, but apparently prefer mud (Coleman 1975) to clean coral substrata (R.C. Willan personal observation). Normally these anaspeideans crawl using cilia on the foot sole and outer surfaces of the parapodia. They graze on green algae (Morton & Holme 1955; Willan & Morton 1984; Gosliner 1987a). In Britain, Thompson & Seaward (1989) have demonstrated that *A. bullata* can change its diet seasonally, switching from ingesting sediment in autumn through spring, to green algae (*Enteromorpha*) in summer. Disturbed animals rise off the substratum and swim with rapid, jerky movements of their bell-like parapodial cloak; this opening and forceful closing of the parapodia resembles the pulsations of a small jellyfish. Swimming can be sustained for up to half an hour. Coleman (1975) commented on the apparently cyclic nature of *A. soluta* populations, and noted that the species can be rare in a given location for many years, then suddenly its numbers increase dramatically.

Superfamily APLYSIOIDEA

Family Aplysiidae

Some members of this family are among the best known of all opisthobranchs because of their intertidal occurrence, abundance, ubiquity and very large size (Fig. 16.57; Pl. 34.4). The perception that the distinct head with its large, erect, grooved rhinophores is hare-like has led to their widely used common name 'sea hare'. Sea hares show a very considerable form range and adaptive radiation. Modifications of the foot and parapodia are indicative of the main evolutionary lines in the series (Fig. 16.1A).

References to sea hares in the literature extend back over 2000 years and studies continue unabated today. The scientific literature is voluminous on almost every aspect of their anatomy, taxonomy, ecology, behaviour and physiology. Eales' memoir (1921) and taxonomic revision (1960) of the genus *Aplysia* are important sources for the first two facets whereas Kandell's book (1979) and Carefoot's comprehensive review (1987a) have summarised information relating to the latter three. Allan (1932, 1941) gave brief popular accounts of the sea hares of Australia. Eales (1960) established names for the Australian species of *Aplysia*. Bebbington (1977) reviewed the Anaspeidea from eastern Australia. Wells (1986) redescribed the Western Australian species, *Aplysia gigantea*. Few ecological data are available for any Australian sea hare. All nine genera in the family are represented in Australian waters.

The sea hares are clearly holophyletic, however, no generally acceptable scheme for grouping the genera has emerged. Traditionally, most emphasis has been placed on the nervous system. The older scheme, favoured here, recognises one family, the Aplysiidae. The two subfamilies, Aplysinae and Notarchinae, are distinguished by long or short pleurovisceral cords, respectively (Burn 1989). An alternative scheme recognises four separate families – Aplysiidae, Dolabellidae, Dolabriferidae and Notarchidae (Boss 1982).

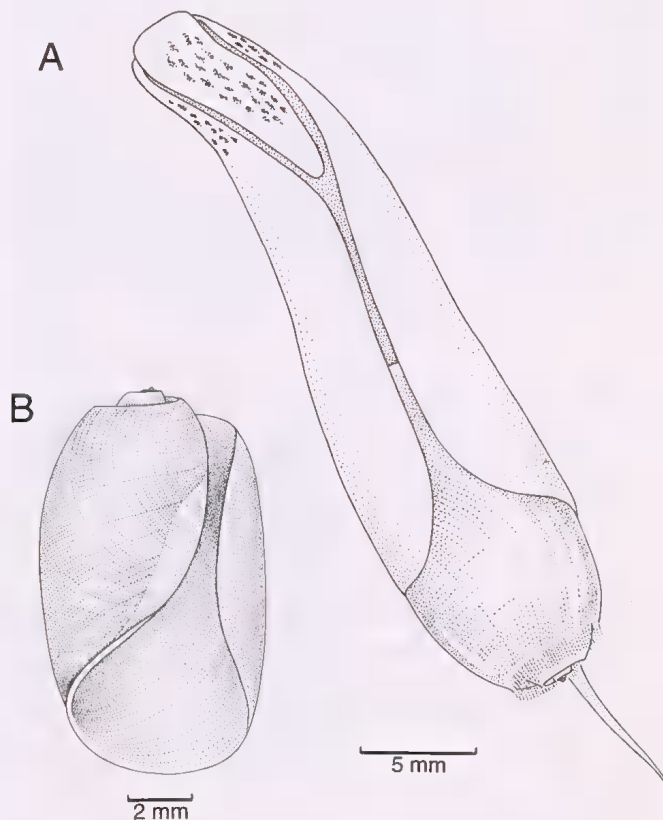


Figure 16.56 Family Akeridae. *Akera soluta*: A, animal, dorsal view; B, shell, apertural view. (A, after photograph by W.B. Rudman) [R. Plant]

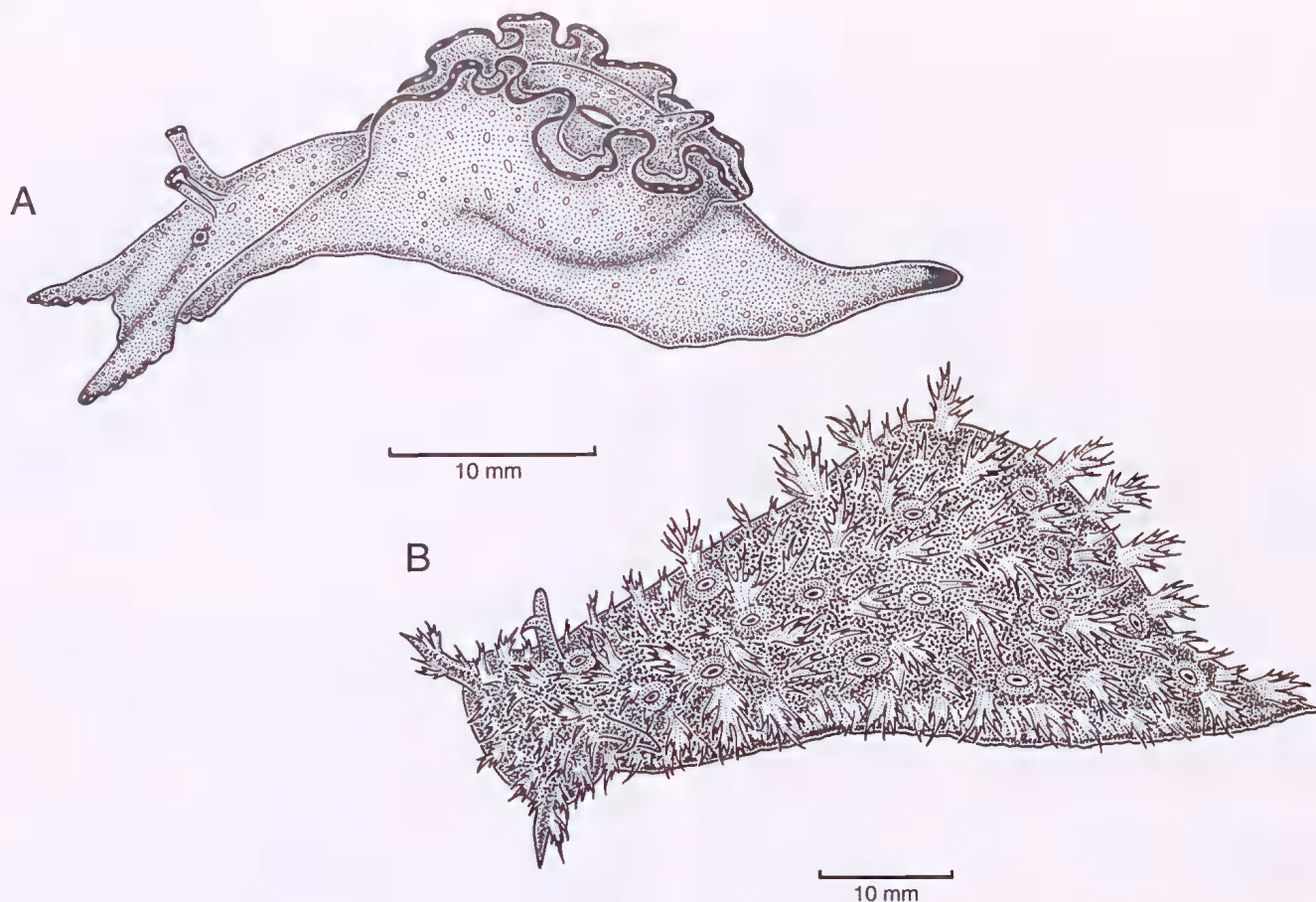


Figure 16.57 Family Aplysiidae. A, *Aplysia parvula*, dorso-lateral view. B, *Bursatella leachii*, dorso-lateral view. (After photographs by R.C. Willan) [L. Newman]

Adult sea hares range from 10–750 mm in length. Body shape is variable. An internal shell is present in *Dolabella*, *Aplysia*, *Syphonota*, *Dolabrifera*, *Phyllaplysia* and *Petalifera*. The thickened and coiled form of the shell in *Dolabella* is interpreted as the primitive condition. The shell is thin and plate-like in *Aplysia* and *Syphonota*, and reduced to a vestigial calcareous wedge in *Dolabrifera*, *Phyllaplysia* and *Petalifera*. It lies beneath the integument in all but *Aplysia parvula* and *A. punctata*, where a mantle foramen leaves part of the shell permanently exposed. *Stylocheilus*, *Bursatella* and *Notarchus* lose their shell completely when they metamorphose. Sea hares move by a creeping action (monotaxic prograde) of the muscular foot, by deliberate swimming in some *Aplysia* species (Fig. 16.9A; Hamilton & Ambrose 1975) or by uncoordinated ‘somersaulting’ in *Notarchus* (Martin 1966; Bebbington & Hughes 1973; Vine 1986). The parapodia generate the propulsive force for swimming or ‘somersaulting’. Brace (1977c) described the musculature of the head and foot.

The gut consists of a muscular pharynx containing the radula and two jaws, long tubular salivary glands, oesophagus, muscular gizzard containing many cuticularised plates, stomach, digestive gland, caecum and long looped intestine. Fretter & Ko (1979) showed there is a sophisticated ciliary sorting mechanism in the stomach. The tufted plicate gill forms a crescent across the mantle cavity. The circumoesophageal nerve ring exhibits different degrees of separation of the ganglia, but in most species the cerebral ganglia are contiguous within a connective tissue sheath or completely fused into a flat band. The pleural and pedal ganglia are always separated, though they may lie together; the visceral pair are either separated or fused. The reproductive system consists of an ovotestis, hermaphrodite duct, nidamental complex (consisting of entwined mucous and albumen glands), and the receptaculum seminis, wide distal duct, bursa copulatrix, external ciliated groove and retractile penis. The most complete accounts of the structure and function of the reproductive system are those by Thompson & Bebbington (1969) for *Aplysia*, Thomas (1975) for *Bursatella* and Fretter & Ko (1984) for *Dolabella*. Reproductive physiology has been investigated by Lederhendler

(1977a, 1977b) and Lederhendler & Tobach (1977). The spawn is an elongate cord, looped into a tangle by movements of the head as it is deposited; its sticky outer surface binds and anchors the mass. Egg production is enormous; Boss (1982) gives a figure of 180 million eggs, which represents one animal’s total output, since sea hares live no more than one year. Larvae are obligate planktotrophs (Switzer-Dunlap & Hadfield 1977, 1979); the only known species with direct development is *Phyllaplysia taylori* from the eastern Pacific (Bridges 1975). Apparently larvae can remain competent to metamorphose in the plankton for longer than 200 days (Kempf 1981), during which time they may be dispersed great distances by ocean currents.

Numerous field studies give a picture of sea hares as highly ‘r-selected’ opportunists (for example, Smith, S.T. & Carefoot 1967; Carefoot 1967, 1970, 1985, 1987a, 1987b; Willan 1979a). Individual sea hares are relatively inefficient at converting ingested food into tissues, but they achieve rapid growth by bulk consumption of green or red algae rather than skill in selective absorption (Willan 1979a). Using five different approaches, Vitalis, Spence & Carefoot (1988) showed experimentally that gut bacteria contribute significantly to nutrition and growth in *Aplysia*.

Aplysia are widely used in neurophysiological experimentation because of their accessible avascular central nervous system, the large nerve cell bodies, the separate ganglia, the clear distinction between the synaptic region and the cell body, and the long pleurovisceral cords. Its relatively unspecialised diet also makes it a good laboratory animal. Consequently there is now a wealth of information on learning, memory, chemoreception, circadian rhythms, arousal, motivation and hormonal control of reproduction in *Aplysia* (for example, Audesirk & Audesirk 1977; Kandel 1979; Carew, Hawkins & Kandel 1983; Ferry 1986).

The demand for captive-reared animals for such trials in place of field-collected ones has stimulated studies on larval development; the results have been most impressive (Strength & Blankenship 1978; Switzer-Dunlap & Hadfield 1979; Paige 1986), despite the long duration of the planktonic phase (approximately 30 days).

Nowadays the major laboratories raise their own animals with generation times as short as 19 weeks (Kriegstein, Castelluci & Kandel 1974; Nolen *et al.* 1995). Artificial diets have been tried with some success (Carefoot 1980, 1982).

Toxins in the skin, opaline gland fluid, purple 'ink' and the digestive gland of sea hares, deter most natural predators (Willan 1979a; Dimatteo 1981, 1982; Carefoot 1987a; Nolen *et al.* 1995), but not humans. Adult *Dolabella auricularia* are eaten in the Society Islands (Boss 1982) and Philippines (Pauly & Calumpong 1984), and the spawn of this species is sold in Fiji (R.C. Willan personal observation). Some toxins are derived from pigments in the food plants (Chapman & Fox 1969; Doty & Aguilar-Santos 1970: summarised by Carefoot 1987a).

About 20 species of sea hares are known from Australia; three-quarters of these belong to the genus *Aplysia*. Three eurythermal species of *Aplysia* are now recognised as being cosmopolitan, *A. parvula* (Fig. 16.57A), *A. dactylomela* and *A. juliana*. Five others are supposedly endemic, *A. cronullae*, *A. denisoni*, *A. extraordinaria*, *A. gigantea*, *A. sydneyensis* (Pl. 34.4), though in view of their long-lived larvae and high vagility, a critical taxonomic review might reduce the size of this endemic group. Other widespread Indo-Pacific warm water species are *Dolabella auricularia*, *Dolabrifera dolabrifera*, *Bursatella leachii* (Fig. 16.57B), *Stylocheilus longicauda* and *Notarchus indicus*. The family is clearly centred in the tropics and within Australia the majority of species live and reproduce in tropical and warm temperate waters.

Order NOTASPIDEA

The Notaspidea is a comparatively small order of opisthobranchs with diverse body forms. Three autapomorphies can be recognised as features unifying the order. A bipinnate gill is present on the right side between the mantle and foot, and gives rise to the common name of side-gilled sea slugs. There are two pairs of enrolled cephalic tentacles, the oral tentacles and rhinophores, and an outgrowth of tissue between the anterior pair of tentacles produces an oral veil.

The bipinnate gill is not considered to be homologous with the anaspidean plicate gill or the mid-dorsal nudibranch gill (Morton 1972, 1979). The broad radula consisting of simple teeth and possession of a shell are symplesiomorphies. The shell has been variously modified or lost in each subfamily. Figure 16.2E shows a diagrammatic representation of the general body form for the order. The variation on this theme and in body form and internal organisation indicate that the order is an ancient one that arose from cephalaspideans or basal heterobranchs independently from the nudibranchs.

Minichev & Starobogatov (1978, 1984) and Schmekel (1985) split the Notaspidea into two orders on the basis of the mantle/gill complex, protoconch and nervous system, but Willan (1987a)

argued for continued unity of these taxa as a natural, holophyletic unit. Thompson's alternative name Pleurobranchomorpha for the order, for conformity with Bullomorpha and Aplysiomorpha, has not gained acceptance. Burn (1962a) revised the New South Wales and Victorian Pleurobranchidae and Thompson (1970) redescribed 10 eastern Australian notaspidean species.

The order includes two superfamilies, separated on the basis of the form of the shell and modifications to the anterior alimentary tract, and the form of the seminal groove. The Tylodinoidea includes forms with an external, limpet-like shell, a cuticularised labial ring lining the pharyngeal bulb, and an open seminal groove; it comprises two families, the Tylodinidae and Umbraculidae. The Pleurobranchinoidea, with the shell internal or absent; two separate jaws within the pharyngeal bulb; and the seminal duct closed, comprises only the Pleurobranchidae.

Superfamily TYLODINOIDEA

This superfamily contains those notaspideans with an external limpet-like shell, a cuticularised labial ring with tessellations on the floor and sides of the oral tube, a stomach which comprises a muscular 'gastric' section with cuticularised ridges internally and a glandular 'pyloric' section, and an open seminal groove, an especially primitive feature. In other respects, the two families, Tylodinidae and Umbraculidae, are highly divergent.

Family Tylodinidae

Members of this family, unquestionably the most primitive of the order Notaspidea, have a limpet-like shell beneath which the animal can generally withdraw. The most unusual anatomical character for a notaspidean is the external sperm groove that leads from the genital aperture at the base of the right oral tentacle to the non-retractile penis. The sole Australian species, *Tylodina corticalis* (Fig. 16.58), was originally placed in the genus *Umbraculum*. Burn (1959) transferred it to *Tylodina* and subsequently described its external features and anatomy (Burn 1960b). Other major anatomical studies were made on non-Australian species by Vayssi re (1885), MacFarland (1966) and Ev. Marcus (1985). *Anidolyta*, the only other genus in the family, does not occur in Australian waters.

When extended, the smooth, bright yellow body of *Tylodina corticalis* can attain 50 mm in length. The thin and rather fragile shell is conical and broadly oval. It has an anisostrophic, or asymmetrically coiled, protoconch with one and a half whorls close to its centre (Willan 1987a). The whitish shell has about a dozen, dark, radial ridges on its upper surface. Internally, the shell is attached to the foot by a ring of muscles. This ring is broken on the right side by a gap in which the intermediate suspensor muscle is located. The anterior end of the broad foot is deeply bilobed and its upper lobe is notched vertically. The head bears two pairs of longitudinally slit tentacles, the anterior (oral) pair of which has a sheet of tissue connecting the bases.

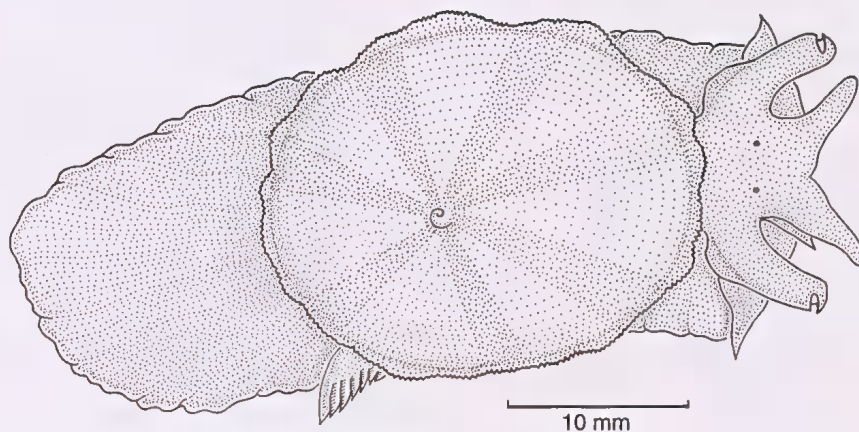


Figure 16.58 Family Tylodinidae. *Tylodina corticalis*, dorsal view. (After photograph by R.C. Willan)

[L. Newman]

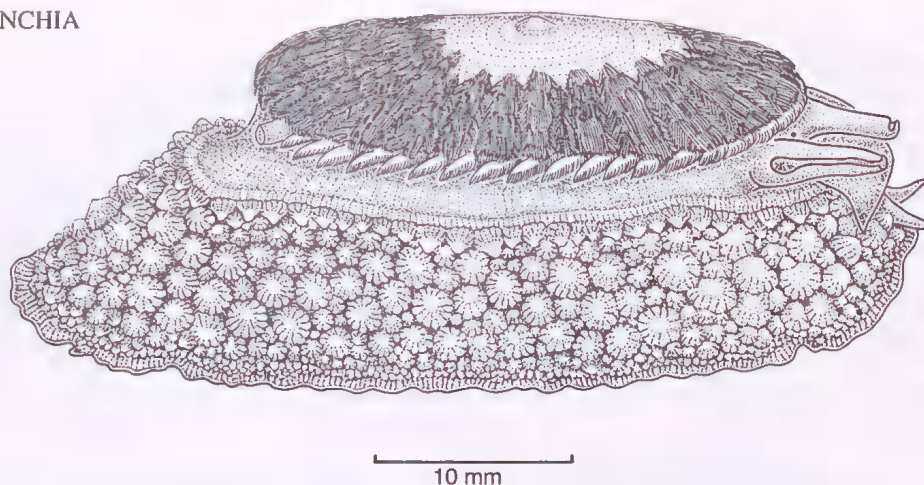


Figure 16.59 Family Umbraculidae. *Umbraculum umbraculum*, lateral view. (After photograph by R.C. Willan)

[L. Newman]

The cuticularised ring of the oral tube has numerous, irregular, thickened polygons towards its anterior end, replaced by dorsally longitudinal ridges. Every row of the radula consists of approximately 260 lateral teeth plus one central tooth. Each lateral tooth bears a single denticle at the base of the main cusp. The muscular part of the stomach bears an armature of cuticularised longitudinal ridges. The anus opens just above the hind end of the gill's basement membrane. There are about 12 pinnae on each side of the rachis in the small, bipinnate gill present on the right side of the body between the mantle and foot. The renal pore opens close to, and just above, the anterior end of the gill. The kidney is a thin-walled sac which lies dorsally within the anterior section of the body cavity and extends backwards on the right side.

The organisation of the nervous system has been described fully by Vayssi re (1885) and MacFarland (1966). MacFarland reported the presence of an osphradium (a small patch of highly sensory epithelium) adjacent and antero-ventral to the anterior end of the gill rachis. The osphradium is innervated by a special ganglion located immediately beneath it. The circumoesophageal nerve ring exhibits a marked concentration of the six main ganglia around the oesophagus; only the visceral ganglion retains its integrity (MacFarland 1966; Gosliner 1981a).

The reproductive system of *Tylodina* is monaulic. The hermaphrodite duct connects with the nidamental glands before passing through the musculature of the right body wall to the genital aperture. The bursa copulatrix also opens at the same site. A short, ciliated, external groove leads from the genital aperture to the non-retractile penis that is situated below the base of the right oral tentacle. The life history is not known for any species of *Tylodina*. Thompson (1970) reported that *T. corticalis* laid a spirally wound spawn ribbon that was bright yellow and contained creamish ova measuring 90 µm in diameter.

Tylodina corticalis, the sole Australian representative of the family, feeds only on sponges of the family Aplysinellidae, order Verongida (Willan 1984a). It lives in open habitats where there is no silt in the water. Although specimens are occasionally found alive in the intertidal zone, *T. corticalis* is predominantly subtidal to a depth of at least 165 m. Recent discoveries by divers of specimens off Bundaberg, Queensland, and the Recherche Archipelago, Western Australia, indicate that the species ranges continuously from southern Queensland around the southern Australian coastline to southern Western Australia.

Biogeographically, *Tylodina* is an enigmatic genus. Four other species occupy restricted areas in temperate waters in other parts of the world – *T. perversa* in the eastern Atlantic and Mediterranean, *T. americana* in the western Atlantic, *T. fungina* in the eastern Pacific and *T. alfredensis* in southern Africa. Only minor anatomical differences separate these species and information on ecology and life history could be helpful in establishing their validity.

Family Umbraculidae

The flattened shell, tubercle-laden body, deep mid-anterior cleft, non-retractile penis, two pairs of oral tentacles, long crescentic gill and the posterior location of the anus are only some of the unique features of *Umbraculum umbraculum*, arguably the most highly derived notaspideans (Fig. 16.59).

Moquin-Tandon's (1870) monograph is still the principal reference for detail on comparative anatomy of *Umbraculum*. Some of the inaccuracies concerning the reproductive system introduced by Moquin-Tandon have subsequently been corrected by O'Donoghue (1929), Ev. Marcus & Er. Marcus (1967b) and Ev. Marcus (1985). Physiological and histological studies are required urgently to elucidate the functional significance of the component parts of the complicated reproductive system. Thompson (1970) gave a short account of the species in eastern Australia.

Umbraculum umbraculum is a large opisthobranch, which can reach 28 cm in diameter. The body is firm and bulky, and bedecked with soft, non-retractile tubercle-like warts. The skin lacks acid-producing glands (Thompson & Colman 1984). The deep, vertical, mid-anterior cleft in the body and foot accommodates the permanently protruded penis, mouth, and oral tentacles. The circular sole of the foot is flat and smooth, and there is no pedal gland at the rear. Colouration is very variable, ranging from dirty grey to brown to yellow or orange or even reddish. A flattened, circular, calcareous shell surmounts the body and is the basis for the common name of umbrella shell. The shell is considerably smaller than the body. Its undersurface bears a complete ring of muscle scars. The protoconch is like that of *Tylodina* (Willan 1987a). The gill lies in a tubular cavity formed by the overlapping mantle and the thinly prolonged margin of the foot, its axis projecting from the body wall; the afferent branchial vessel runs along its mesial edge and the efferent vessel along the exposed lateral edge. The gill has no distinct lateral ciliary tracts and the cilia that are present simply remove lodging particles and distribute mucus (Morton 1972).

The mouth opens via a non-protrusible pharynx below the penis, within the pedal cleft. The cuticular lining of the oral tube consists of numerous, minute, polygonal plates. The radula is extremely broad; Ev. Marcus (1985) calculated a total of about 800 000 teeth for a preserved specimen, measuring 95 mm long. All teeth are tiny, simple, curved hooks, arranged in rows of about 2500. The cuticularised, transverse ridges that line the stomach are quite unlike the conical gizzard plates of sea hares. The two ducts of the digestive gland enter the stomach posteriorly close to the point of emergence of the intestine. The intestine loops in a circle and the anus opens far back on the right side via a tubular rectum. The circumoesophageal nerve ring displays the same concentration of ganglia behind the pharyngeal mass as in the Tylodinidae, but in *Umbraculum* the pleural and oesophageal ganglia have fused and the visceral ganglion is not discrete. The penis is most peculiar; it

resembles an enrolled leaf, lies in the pedal cleft and is not retractile. Spermatozoa have an enormously lengthened nucleus and the centriolar derivative and anterior end of the mitochondrial derivative are close to the acrosome (Healy & Willan 1984).

The spawn mass is a tightly spiralled, heavily pleated coil. Within the mass, clusters of 12 to 45 eggs are grouped into capsules. A single mass can contain from 100 000 to 4 500 000 eggs (Hartley 1964; Thompson 1970). There are no data on development.

Umbraculum is a slow and ponderous opisthobranch. It eats a diverse range of demospongiid sponges, but as yet, sponges belonging to the orders Verongida (the food of *Tylodina*) and Dictyoceratida are absent from those recorded as food (Willan 1984a). *Umbraculum* lacks a protrusible pharynx, and when feeding, presses its mouth (in its cleft at the anterior end of the foot) directly onto the food (Willan & Morton 1984). *Umbraculum* apparently lives for longer than one year (but probably less than two) and thus is a notable exception among the generally annual Opisthobranchia (Willan 1984a).

The majority of opisthobranch systematists maintain that there is only a single species in the family, *Umbraculum umbraculum*, with a cosmopolitan distribution throughout tropical and warm temperate Indo-Pacific seas (for example, Burn 1959; Rehder 1980; Boss 1982). Curiously, this opisthobranch has not yet been found in a number of localities in the high tropics despite many years of searching. It is known from all Australian states except Tasmania.

Superfamily PLEUROBRANCHOIDEA

Family Pleurobranchidae

The Pleurobranchidae are side-gilled sea slugs with no external shell and with or without an internal shell (Fig. 16.60; Pl. 33.7). Other characteristics are the trapezoidal veil between the oral tentacles immediately above the mouth, longitudinally slit oral tentacles and rhinophores, a posterior pedal gland on the foot sole, a median buccal gland, and a retractile penis immediately in front of the gill on the right side. Willan (1987a) reviewed the higher classification critically and recognised eight genera, all but two of which (*Pleurehdera* and *Bathyberthella*) are known to occur in Australian coastal waters. An additional genus, *Tomthompsonia*, was described from Antarctica in 1991 (Wägele & Hain 1991; see also Hain, Wägele & Willan 1993).

Knowledge of pleurobranchs rests on firm anatomical foundations, contributed primarily by Lacaze-Duthiers (1859), Bergh (1897, 1898, 1902b, 1905a), Vayssière (1898, 1901), Odhner (1939) and MacFarland (1966). Burn (1962a) and Thompson (1970) have described Australian species, several of which also occur in New Zealand (Willan 1983). Developmental

studies were conducted outside Australia by Gohar & Abul-Ela (1957), Usuki (1969) and Tsubokawa & Okutani (1991), and Healy & Willan (1984, 1991b) described sperm ultrastructure in representatives of five genera. No ecological studies have as yet been conducted in Australia.

The family contains two divergent lineages, each considered as a subfamily, the Pleurobranchinae and the Pleurobranchaeinae. In the Pleurobranchinae, the rhinophores are situated side by side on top of the head, the mantle entirely roofs the body and a shell is present beneath the mantle. No member of this subfamily has a shell that is wholly or partially uncovered in life (Willan 1978b), but sometimes the shell is lacking in specimens of a species that normally has one. The shell is anchored, both anteriorly and posteriorly, to the body wall by dorso-ventral muscles (Brace 1977c). In the Pleurobranchaeinae, the rhinophores have been displaced to the sides of the head, and fusion has occurred anteriorly between the oral veil and mantle with consequent oral veil enlargement and mantle reduction. A shell is never present.

The Indo-Pacific species, *Pleurobranchus grandis*, the largest known pleurobranch, can attain 200 mm in length when it is crawling. Locomotion is brought about by cilia on the foot sole beating on a mucous sheet produced by the anterior pedal groove. The capacity for sustained swimming has evolved independently in one species from each subfamily – the North Atlantic *Pleurobranchus membranaceus* (Fig. 16.9B; Thompson & Slinn 1959) and the Indo-Pacific *Euselenops luniceps* (Pace 1901). *Pleurobranchaea* can lift off the substratum by powerful vertical flexions of its body, but it cannot keep swimming. All pleurobranchs secrete acidic fluids from holocrine epidermal glands and/or multi-cellular subepidermal glands (Marback & Tsumamal 1973; Thompson & Colman 1984) for their own defence.

The gut, which is relatively unspecialised, consists of a protrusible oral tube, a muscular pharyngeal bulb, a median buccal (= poison or acid) gland, two narrow and tubular salivary glands with bulbs, a broad and sometimes specialised radula, two jaws composed of interlocking cuticularised elements, an oesophagus, thin-walled crop and stomach, digestive gland, relatively short intestine, and rectum. The anus opens above, and towards the hind end of, the gill. Willan (1984b) remarked on the extent of intraspecific variability in the sculpture of the masticatory elements in the Pleurobranchinae. Morse (1984) described the mechanics of feeding in *Pleurobranchaea*. The median buccal gland, which can occupy a large portion of the visceral cavity, secretes a strongly acidic fluid (pH = 1.2), presumably for immobilisation of prey.

The genus *Pleurobranchaea* has many of the attributes of the sea hare *Aplysia*, such as its non-specific diet and hardness under laboratory conditions, so its nervous system and behaviour have been studied extensively (reviewed by Kandel 1979).

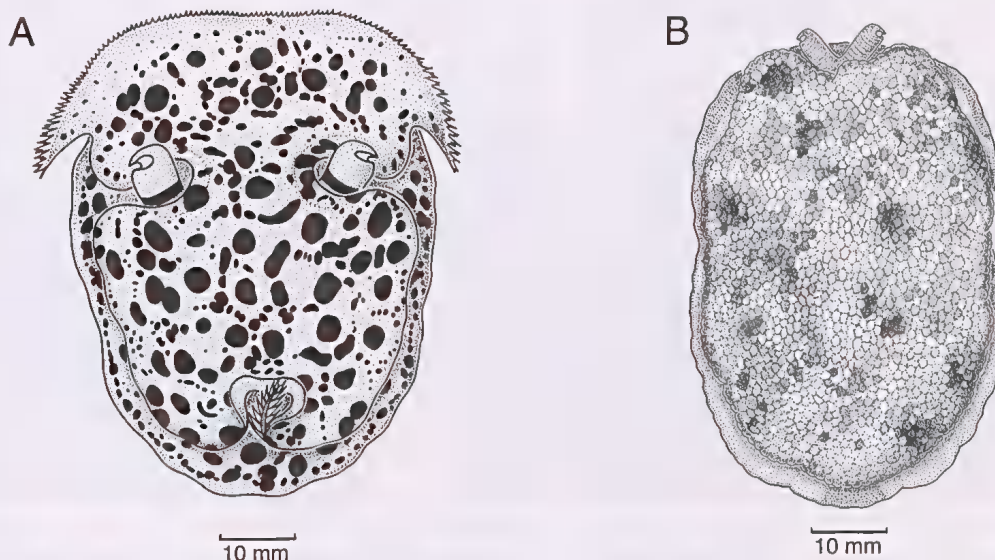


Figure 16.60 Family Pleurobranchidae. A, *Euselenops luniceps*, dorsal view. B, *Pleurobranchus peronii*, dorsal view. (After photographs by R.C. Willan)[L. Newman]

16. OPISTHOBRANCHIA

Pleurobranch reproductive systems are complicated, being dialuc in the Pleurobranchaeinae and triaulic in the Pleurobranchinae. This triaulic is not homologous with that found in dorid nudibranchs. Spawn consists of spiral ribbons containing many eggs, each in its own capsule. Larvae of all species are obligate planktotrophs as far as is known. Pleurobranchs have an annual life cycle (Usuki 1969).

Willan (1984a) reviewed the literature on diets. *Berthella* species eat sponges; *Berthellina* species also eat sponges, as well as corals occasionally and possibly sea anemones. *Pleurobranchus* species eat ascidians, whereas *Pleurobranchaea*, and apparently *Pleurobranchella*, species are opportunistic carnivores that accept a range of soft-bodied invertebrates, such as hydroids, anemones, polychaete worms and molluscs. Apparently *Tomthompsonia* is a non-selective deposit feeder (Hain, Wägele & Willan 1993). Pleurobranchs tend to be solitary and nocturnal, but in *Pleurobranchaea* at least, animals are known to hunt in daylight. Food is located by chemotaxis over long distances, and by the oral veil over short distances. Adult *Pleurobranchaea* can be highly pugnacious and will often bite a partner prior to mating (Willan 1983). Large animals will cannibalise smaller ones.

The Pleurobranchidae are essentially a tropical family. However two species, *Bathyberthella antarctica* and *Tomthompsonia antarctica* occur in Antarctica. In Australia, ten species live in tropical and six in temperate waters. All the tropical species are widely distributed in the Indo-West Pacific. Two of the six temperate species, *Pleurobranchus hilli* and *Berthella serenitas*, are endemic to Australia, whereas *Berthella medietas* and *Pleurobranchaea maculata* also occur in New Zealand. The two remaining species have very wide distributions – *Berthella stellata* occurs circumglobally in tropical and warm temperate seas (Gosliner & Bertsch 1988), and *Berthellina citrina* occurs throughout the Indo-Pacific (Willan 1983).

Order THECOSOMATA

The molluscs known for many years as pteropods were separated by Blainville (1824) into two groups: the shelled Thecosomata, and the naked or shell-less Gymnosomata. These are now recognised to be quite unrelated opisthobranch groups which have evolved in parallel, to become holoplanktonic. Thecosomes are usually epiplanktonic, occurring in all oceans and being most diverse in tropical and subtropical seas (Solis & von Westernhagen 1978). Only a few species are bathypelagic. Despite being an abundant component of plankton communities, few studies have been made on the distribution and ecology of thecosomes or gymnosomes in Australian waters.

At least 13 thecosome genera and 60 species are known from the world's oceans (van der Spoel 1976). Approximately half of the species are found in Australian waters, the family Cavoliniidae being most diverse, its members most abundant (Newman & Greenwood 1987; Newman 1990). Thecosomes vary in size from the small limacinids (usually less than 2 mm in shell height) to *Corolla*, the largest with a wingplate expansion of up to 80 mm. The animal and its shell are coiled sinistrally in the families Limacinidae and Peraclididae, and are bilaterally symmetrical in the families Cavoliniidae, Cymbuliidae and Desmopteridae.

Meisenheimer (1905) divided the Thecosomata into two suborders, the Euthecosomata and the Pseudotheosomata. Euthecosomes are known as sea-butterflies because they have two 'wings' (= parapodia) which protrude from the aperture of the shell. The wings are derivatives of the gastropod foot (Fiege 1990). The animal can withdraw completely into the aragonitic shell. In pseudotheosomes, the wings are fused into a fixed wingplate and many species have a bilaterally transparent pseudoconch composed of conchiolin. Two pseudotheosome families lack a pseudoconch. The Peraclididae have a calcareous shell coiled sinistrally (similar to the euthecosome family Limacinidae), and the Desmopteridae are shell-less.

The mouth, bordered by pairs of lips, is situated between the wings in euthecosomes and extends into a proboscis in pseudotheosomes. The oesophagus leads into a gizzard which is armed with plates for the mechanical breakdown of planktonic prey. The radular formula is consistently 1-1-1 in euthecosomes and (1)-1-1-1-(1) in pseudotheosomes. A small jaw is found above the radula.

Respiratory exchange is thought to occur across the wing surface in the majority of species. Gills are found in all peraclidids but in only a few cavoliniid species. Sense organs include tentacles with eyes at the dorsal side of the neck, two statocysts, and an osphradium (van der Spoel 1967). Details of thecosome anatomy and morphology are given by Boas (1886), Pelseneer (1888a), Meisenheimer (1905) and van der Spoel (1967, 1976).

Field studies have shown that many species feed by using a transparent and delicate mucous 'fishing' web. This web is held above the animal and is used to entrap prey. Eventually the web is pulled into the mouth and food items are sorted. The animal can detach itself immediately from the web if disturbed (Gilmer & Harbison 1986). Thecosomes are planktivorous, and feed primarily on diatoms, dinoflagellates, foraminiferans, or radiolarians (Boas 1886; van der Spoel 1967; Gilmer 1974). Larger zooplanktonic prey items, such as bivalve veligers, heteropods and copepods, have been found among the gut contents of some pseudotheosomes (Meisenheimer 1905). Predators of thecosomes include commercially important fish species (herring, mackerel and salmon), gymnosomes, chaetognaths, seals, whales and seabirds (Meisenheimer 1905; Lebour 1932; Dunbar 1942; Russell 1960; Le Brasseur 1966).

All thecosomes are protandric hermaphrodites. According to van der Spoel (1967), the reproductive systems of thecosomes show little variability. The ovotestis is situated in the apical whorl in species having coiled shells and ventro-caudally in the bilaterally symmetrical species. The genital opening and penis are found on the right side of the neck region. Juveniles develop first into males, then hermaphrodites, and eventually into females. The phenomenon of strobilation (asexual reproduction) has been documented for some cavoliniids (van der Spoel 1973a, 1979; Pafort-van Iersel & van der Spoel 1986). Veligers, with a bilobed velum, usually hatch from free-floating gelatinous egg masses. The few bathypelagic species and one epipelagic limacinid are viviparous and brood their young in a modified mantle cavity (Tesch 1948; Lalli & Wells 1973).

Thecosomes are known to show fidelity to particular water masses, which makes these zooplankters useful hydrological indicators (Wormelle 1962; Chen & Bé 1964; Myers 1968; Chen & Hillman 1970; Furnestin 1979; Newman & Corey 1984; Wormuth 1985; Schalk 1990). Within the living plankton, the shell mass of pteropods may exceed that of foraminiferans (Theide 1975). Swarming behaviour occurs in many limacinids and cavoliniids, and at times these molluscs are an abundant food source for their predators (Bonnievie 1933; Tesch 1946; van der Spoel 1967; Newman & Corey 1984; Newman 1990). Some thecosomes also show strong diurnal vertical migrations; for example, as much as 900 m per day in *Clio* (van der Spoel 1967).

Pelseneer (1888b) was the first to record thecosomes from marine sediments. Shelled pteropods are also known to form a dense deep-sea aragonitic sediment ('pteropod ooze') which is composed mainly of limacinid and creseid shells, as well as atlantid heteropods (Chen 1964). Thecosomes are well represented in the fossil record (Curry 1965; Diester-Haass & van der Spoel 1978; Curry & Rampal 1979; Janssen 1989, 1990). The dissolution of pteropod shells is a major regulating factor in the carbonate system of the oceans (Berger 1978; Betzer, Byrne, Acker, Lewis, Jolly & Feely 1984).

Thecosomes can act as vectors of dinoflagellate toxins. These can cause paralytic shellfish poisoning by their accumulation and subsequent transfer to planktivorous fish (White 1977). Halstead (1965) and Nishimura (1965) reported that bathers developed skin

rashes from swimming amongst swarms of creseids. Thecosomes have also been found to act as hosts for parasitic trematodes (Vande Vusse 1980). Empty shells are known to provide habitats for amphipods, sipunculans and isopods (Just 1977). Abandoned feeding webs also provide food for copepods and contribute to the production of 'marine snow' in tropical waters (Riley 1963; Alldredge 1972; Gilmer 1974).

There are only a handful of records and studies of thecosomes from Australian waters. Pelseneer (1888b) first documented the thecosomes from waters surrounding Papua New Guinea. It was not until Meisenheimer's (1905) worldwide review and Tesch's (1904, 1948) studies in the Indo-Pacific that records from Australian waters became available. Studies dealing with the Australian fauna include those by Russell & Coleman (1935, the northern Great Barrier Reef), Dakin & Colefax (1940, the New South Wales coast), Macpherson & Gabriel (1962, Victoria), Wells (1976, 1978, the Western Australian coast) and in both Australian and Papua New Guinean waters, Newman & Greenwood (1987, 1988), Newman & van der Spoel (1989), Newman (1990) and van der Spoel & Newman (1990).

Thecosome biogeography was reviewed by van der Spoel (1967, 1976) and van der Spoel & Heyman (1983).

Species identification is based primarily on shell surface features such as shape, number of striae and shape of the protoconch. Intraspecific variation is high and the majority of species are represented by distinct geographic forms (van der Spoel 1967, 1976). Specimens should be collected either *in situ* or from short duration plankton tows to prevent damage to their delicate bodies and fragile shells. Shelled species should be preserved and stored in 70% buffered ethanol, to avoid rapid dissolution of the aragonitic shells. Pseudothecosomes should be relaxed and preserved in 3–5% buffered formalin.

Family Limacinidae

This family comprises only the genus *Limacina* (= *Spiratella*) and seven cosmopolitan species. Limacinids have a thin, transparent shell which is usually less than 2.5 mm long (Fig. 16.61), with the exception of *L. helicoides* in which the shell can reach a maximum shell height of 11 mm and diameter of 15 mm (van der Spoel 1967). The operculum is usually lost in adults. The aragonitic shell is extremely fragile (Chen 1964).

Limacinids are found commonly in offshore plankton and, due to their small size, are often confused with caenogastropod veligers. Distinctively, these thecosomes are sinistrally coiled with two wings protruding from the aperture instead of the typical caenogastropod velar lobes. The shell and animal are usually colourless except for a rose, yellow or brown flush around the aperture, suture and footlobes.

This family is thought to be the most primitive of the euthecosomes since the shell and body are coiled. In all other thecosome families the coiling has been lost by detorsion and a secondary bilateral symmetry has developed (Tesch 1946; van der Spoel 1967). The visceral mass is also sinistral and the inhalant and exhalant openings of the mantle cavity are reversed in comparison with most other gastropods. The mantle is dorsal and the gonad is located in the apical whorls. The genital and anal openings are on the right side of the animal. The oesophagus is straight and leads to the gizzard which contains strong plates for mechanical breakdown of phytoplankton (Morton 1954).

The two wings are used primarily in locomotion. The foot is divided into footlobes or lips that surround the mouth and aid in feeding. The wings are covered in forward beating cilia which probably facilitate the transport of food particles to the mouth (Fiege 1990). Gilmer & Harbison (1986) found *Limacina* feeding with a spherical mucous web as observed in cavoliniids and cymbuliids. The web, floating above the animal, is pulled into the mouth along with trapped food items. Feeding and swimming cannot occur at the same time (Gilmer & Harbison 1986). Sinking of the animal can be arrested by this 'fishing' web. When swimming, the animal follows a spiral course with its shell aperture up and wings extended (Morton 1954).

Studies on *L. retroversa* in the Atlantic show that food items include dinoflagellates and diatoms (Lebour 1932). Predators of limacinids include chaetognaths, gymnosomes, salmon, herring, mackerel, seabirds, seals and whales (Meisenheimer 1905; Lebour 1932; Dunbar 1942; Le Brasseur 1966). The thecosomes can escape predation either by swimming away rapidly or by ceasing to swim, holding the wings above the aperture and sinking with a parachute-like action.

The circulatory system is simple and the heart is situated distally to the kidney. Gills are absent and gaseous exchange occurs over the wing surface. Sense organs consist of unequal stalked eyes located dorsally at the neck region, two statocysts, and an osphradium on the left side of the body cavity (van der Spoel 1967).

The ovotestis is situated in the apical whorls and the penis on the right side near the mouth. Copulation of shelled pteropods has not been observed (Lalli & Wells 1978). Eggs are normally laid in the plankton in gelatinous ribbons and the young may hatch within 1–2 days. Late veligers have a bilobed velum and develop a sinistral shell within 2–3 days (Lebour 1932). *Limacina inflata*, by contrast, broods its young in its modified mantle cavity until the veliger stage, and the bathypelagic *L. helicoides* retains its larvae in a specialised mucous gland until they are juveniles (Tesch 1948; Lalli & Wells 1973). Studies on *L. retroversa* in the North Atlantic show that populations reproduce more than once a year, usually in the spring and summer months (Hsiao 1939a, 1939b; Redfield 1939; Newman & Corey 1984).

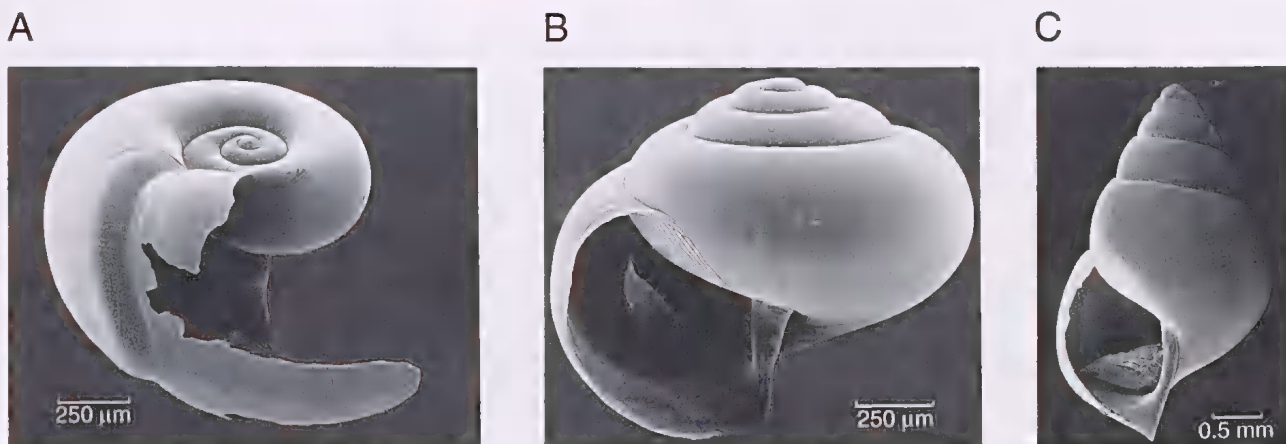


Figure 16.61 Family Limacinidae. Shells: A, *Limacina inflata*, dorso-lateral view; B, *Limacina lesueuri*, apertural view; C, *Limacina bulimoides*, apertural view.

[L. Newman]

16. OPISTHOBRANCHIA

In Atlantic waters, sporadic swarms of *L. retroversa* are known to cause serious problems for herring, cod and haddock fisheries. These fish species feed on large numbers of limacinids. Toxic chemicals in these thecosomes cause rapid decay of the stomach contents and the fish become unmarketable. Such fish are often referred to as 'stinkers' or 'black guts' (Wimpenny 1966). *Limacina retroversa* was also found to concentrate paralytic shellfish toxins and transfer them to predators such as herring, ultimately causing massive fish mortalities (White 1977).

Tesch (1948) found that limacinids were poorly represented in collections from Indo-Pacific waters. He attributed this to the large mesh-size of the plankton nets used because limacinids were caught when the nets became clogged with other plankters. According to van der Spoel (1967), van der Spoel & Heyman (1983), Wells (1983) and Newman (1990), six species commonly occur in Australian waters. *Limacina helicina* is a cold water species restricted to the colder waters around Tasmania and the Subantarctic. The bathypelagic species, *L. helicoides*, has been recorded from south-western and south-eastern continental coasts (van der Spoel 1967; Wells 1983). Three subtropical/tropical species, *L. bulimoides*, *L. inflata* and *L. trochiformis*, are found along the eastern coast. The most common of these is *L. trochiformis* which is found from the Gulf of Carpentaria to the Tasman Sea, and also on the North West Shelf (Newman 1990). Russell & Coleman (1935), like many other authors, misidentified the pseudothecosome genus *Peraclis* as a limacinid, but did not record true limacinids within Great Barrier Reef waters. Virtually nothing is known about the ecology or life histories of limacinids in Australian waters, but several studies have been undertaken elsewhere (Hsiao 1939a, 1939b; Redfield 1939; Lalli & Wells 1973, 1978; Newman & Corey 1984).

Species identification is based on shell shape including the number of whorls, height of the spire and depth of the umbilicus. Meisenheimer (1905) discussed the comparative biology, van der Spoel (1967) reviewed the biogeography, and Lalli & Wells (1978) studied the reproductive biology of limacinids.

Family Cavoliniidae

Cavoliniids are the most diverse and abundant holoplanktonic molluscs in tropical waters. These thecosomes are bilaterally symmetrical with extensive wings and mantle appendages (Fig. 16.62A; Pl. 34.5). Unlike those of limacinids, the thin cavoliniid shell is not coiled, it lacks an operculum, and its shape can be extremely variable (Fig. 16.62B–E). The largest species, *Clio recurva*, can reach 30 mm in shell length (van der Spoel 1967).

Three subfamilies are differentiated on the basis of shell shape. The Clioinae have a needle-like or triangular shell which tapers posteriorly (Fig. 16.62A, D, E). In the Cuvierininae, the shell is distinctively bottle-shaped, whereas in the Cavoliniinae the shell is rounded or globular, with a bivalve-like appearance (Fig. 16.62B, C). Lateral and dorsal spines are present in some species. The caudal spine, representing the protoconch, is often detached or broken. Planktonic adaptation is most advanced in the Cavoliniinae in which the lateral spines and dorsal lip are expanded to form a large floating surface and the shell is broad for increased stability (van der Spoel 1968). Davenport & Bebbington (1990) believed the triangular shell in many cavoliniids acts as a hydrofoil; these pteropods are capable of brief high-speed swimming.

The mouth, situated dorsally in a triangular depression between the wings, is surrounded by three ciliated lobes or lips. The digestive tract is similar to that of limacinids except that coiling of the intestine is reversed. The heart and kidney are found caudally on the left and the anus empties on the left into the pallial cavity. The sexual aperture is on the right side. Gills occur only in the genera *Cavolinia* and *Diacavolinia* (van der Spoel 1967, 1987).

Field observations, show that a spherical mucous web, as found in other thecosomes, is deployed for capturing prey. The net traps phytoplankton and zooplankton, which are compacted with mucus and directed into the mouth by cilia on the surface of the wings. Consumption of the web takes 2–3 minutes. Digestive wastes are formed into strings and channelled out over the dorsal surface of the mantle. These strings have been seen to attract swarms of copepods (Gilmer 1974; Gilmer & Harbison 1986).

Cavoliniids are generalist feeders, and primarily capture diatoms, dinoflagellates, radiolarians and foraminiferans. Prey size depends on the maximum dimensions of the ciliated tracts on the surface of the wings. Cavoliniids cannot feed under laboratory conditions since they are unable to deploy their web (Gilmer 1974).

Locomotion is achieved by flapping the two wings which protrude from the shell aperture. Gilmer & Harbison (1986) observed that many species are neutrally buoyant, supported by their bilobed mucous web. Swimming is used only as an escape response. An extensive external mantle surrounds the entire shell. In *Cavolinia uncinata* the mantle is divided into anterior, dorsal, ventral and medial lobes. The most complex mantle structures occur in *Diacria* and *Cavolinia*. The lobes are normally held perpendicular to the body, and trail behind when the animal is swimming and can be withdrawn intact when disturbed. The mantle lobes act to stabilise the animal by increasing the surface area to arrest sinking (Gilmer 1974; Gilmer & Harbison 1986).

Cavoliniids are protandric hermaphrodites, that develop from males into hermaphrodites, and then into females; more than one male stage can occur. Sexual maturity is usually reached in one year (van der Spoel 1973b). Veligers, with a bilobed velum, hatch from planktonic egg masses (Pl. 34.6) and are surrounded in a mucous sheath. These juveniles possess a fragile shell that is flexible (Newman 1990). Identification of juvenile cavoliniids to species is difficult, as the shells look similar and differ greatly in shape from the adult shell (Troost & van der Spoel 1972). In *Diacria*, *Diacavolinia* and *Cuvierina* the juvenile shell breaks off.

Viviparity has been documented for three bathypelagic species in the genus *Clio*; their encapsulated larvae develop in the mantle cavity (Tesch 1946, 1948), or within an accessory gland (van der Spoel 1967). The unusual phenomenon of strobilation (transverse fission) was reported by van der Spoel (1973a, 1979), and Pafort-van Iersel & van der Spoel (1986). Under laboratory conditions, an aberrant stage is formed by strobilation of a normal individual. The new individual detaches itself from the shell as a naked thecosome, transporting only gonads.

Approximately 25 cavoliniid species are known to occur in Australian waters. Along the eastern coast, massive swarms of *Cavolinia longirostris* and, to a lesser degree, *Creseis acicula* have been reported from the length of the Great Barrier Reef (Tesch 1948; Newman 1990). The most common inshore species occurring along the eastern coast are *Creseis acicula*, *C. virgula* and *C. chierchiae* (Pl. 34.5). Newman (1990) reported on 18 cavoliniid species that were found to be new records or extended species ranges for Australian waters. Other Australian studies include the Siboga Expedition (Tesch 1904), the Dana Expedition (Tesch 1948), Great Barrier Reef Expedition (Russell & Coleman 1935), and work on the Eastern Australian Slope Water (Sheard 1965), and Western Australian waters (Wells 1976, 1978).

Species identification is based primarily on the morphology of the shell, including the shape and size of lateral spines, the shape of the protoconch and the presence of surface striae. Intraspecific variation is most evident in *Cavolinia tridentata*, which is represented by nine forms with different geographic distributions (van der Spoel 1974). Cavoliniid anatomy, reproductive biology, taxonomy and biogeography are reviewed by van der Spoel (1967, 1976) and van der Spoel & Heyman (1983).

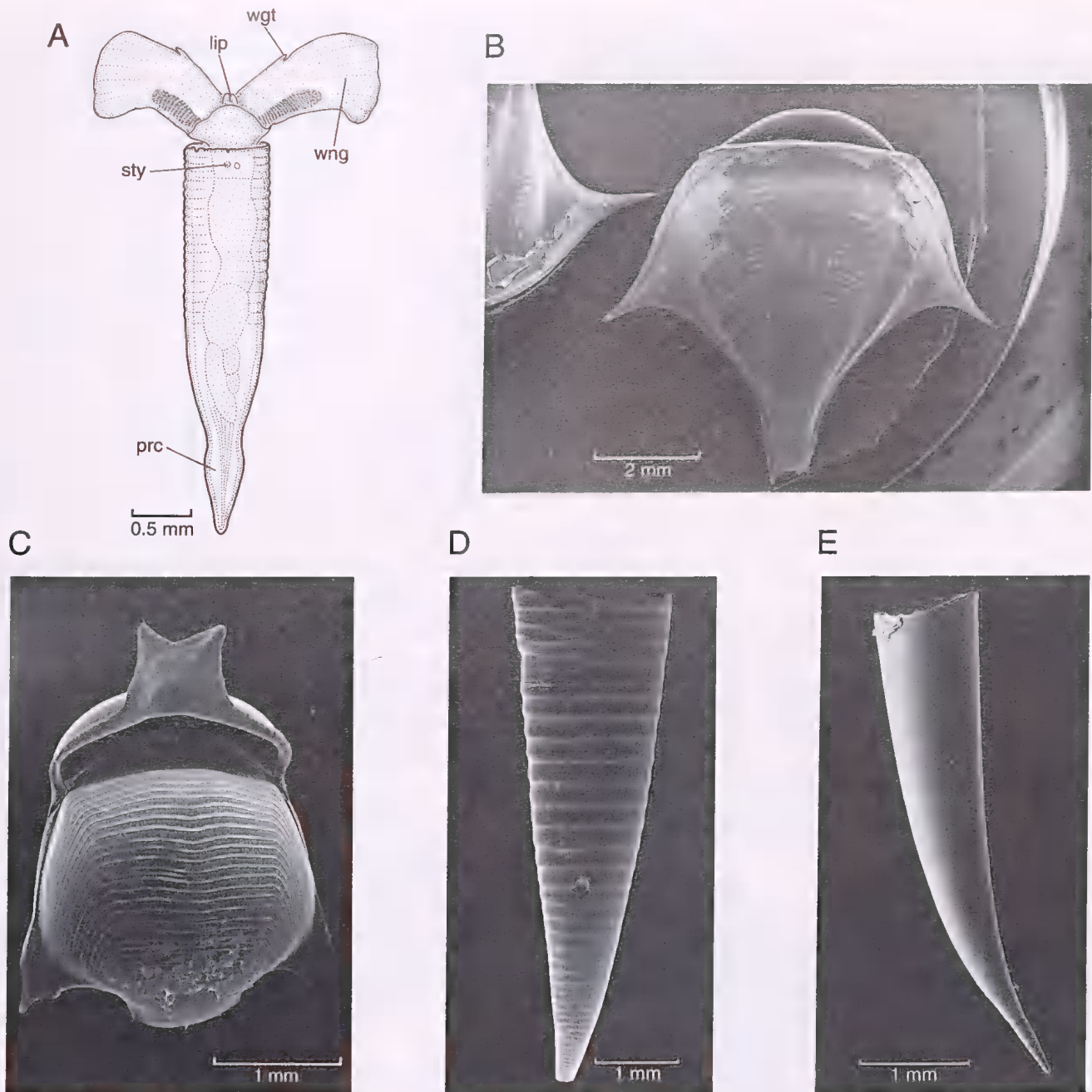


Figure 16.62 Family Cavoliniidae. A, *Creseis chierchiai*, animal, ventral view. B–E, variation in shell form: B, *Diacria trispinosa*, ventral view; C, *Diacavolinia longirostris*, ventral view; D, *Hyalocyclus striata*, lateral view; E, *Creseis virgula*, lateral view. lip, lips; prc, protoconch; sty, statocyst; wgt, wing tentacle; wng, wing. [L. Newman]

Family Peraclididae

Peraclidids are shell-bearing pseudothecosomes which have a sinistrally coiled shell and a fringed gill. They are often confused with the euthecosome genus *Limacina*, in which the shell is also sinistral, but the presence of a wingplate places peraclidids firmly within the Pseudothecosomata. Peraclidids are generally mesopelagic or bathypelagic in distribution. The family is monogeneric with nine species, and little is known of the biology and ecology of these deep-dwelling thecosomes.

The operculate shell, usually less than 7 mm in length, is extremely fragile; it has approximately five whorls with a distinctive rostrum on the ventral rim (Fig. 16.63). The fringed gill is attached to the left side of the mantle cavity and protrudes from the right side. The heart, kidney and renal opening are located in the anterior portion of the mantle cavity (van der Spoel 1976).

Peraclidids have a well-developed jaw and gizzard with five plates which are used for the mechanical breakdown of their prey. The radular formula is (1)-1-1-1-(1). Field studies have shown that *Peraclis reticulata* also feeds by producing a mucous web or sheet

(Gilmer & Harbison 1986). Live *P. reticulata* can set a funnel-shaped mucous sheet reaching up to 50 mm in diameter. The mouth, surrounded by a short proboscis, is raised and projects ventrally. The mucous sheet is used for trapping planktonic prey which are then pulled into the mouth along with the mucus. The apertural rostrum provides a funnel through which the digestive wastes are channelled away.

The wings, fused into a wingplate, are held above the body. Locomotion is slower than in euthecosomes; the wingplate produces a sculling-like motion for swimming. These zooplankters are neutrally buoyant when feeding, due to their extensive mantle and feeding mucous sheet (Gilmer & Harbison 1986). Peraclidids can jerk free of their mucous sheet, when disturbed, and then swim downward. Attempts to keep these animals alive in the laboratory have failed consistently, probably due to the restriction of their movement and inability to feed in confinement (Gilmer 1974).

Peraclidids are protandric hermaphrodites. The veligers have a sinistral limacinid-like shell.

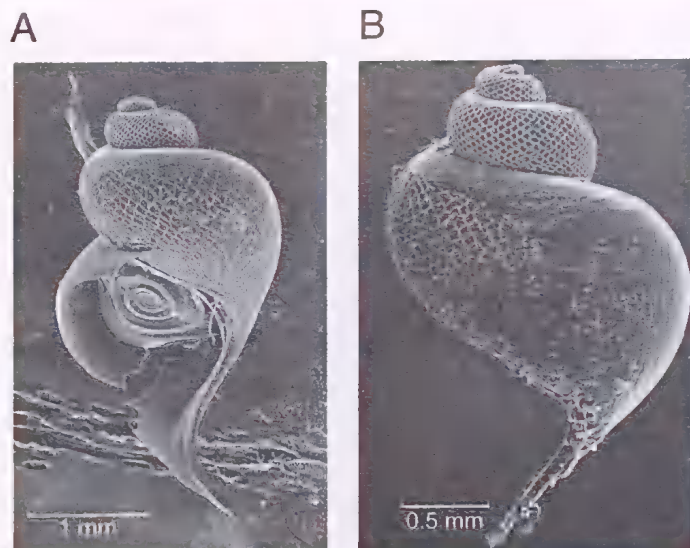


Figure 16.63 Family Peraclididae. *Peraclis reticulata*, shell: A, lateral view, showing the apertural rostrum; B, dorsal view. [L. Newman]

Within Australian waters, peraclidids are rare; there are few records of their occurrence. *Peraclis reticulata*, the most common species, is recorded from waters off New South Wales and northern Western Australia (van der Spoel 1976; Newman 1990). *Peraclis reticulata* is thought to be primarily mesoplanktonic, being found below 100 m, although Gilmer & Harbison (1986) have observed it at depths of 35 m. Two other species, *P. apicifulva* and *P. moluccensis*, share a similar distribution with *P. reticulata*, whereas *P. valdiviae* is only known from waters off New South Wales (van der Spoel 1976). All other species appear to be either mesopelagic or bathypelagic.

Shell identification is based primarily on the flaring and number of protrusions of the apertural lip. *Peraclis reticulata* is distinguished by the reticulate pattern on the spire and dorsal surface of the last whorl (Fig. 16.63). Field observations of living specimens are required to further understanding of pseudotheosome ecology and behaviour. Van der Spoel (1976) reviewed the taxonomy and distribution of this family, and feeding biology is discussed by Lalli & Gilmer (1989).

Family Cymbuliidae

Members of the family Cymbuliidae have no calcareous shell as adults. The animal fits into a transparent, slipper-like pseudoconch of conchiolin and the body is attached only by muscles and the mantle membrane (Fig. 16.64). The pseudoconch provides stability as well as buoyancy for the animal (Fig. 16.64B; Davenport & Bebbington 1990); it is not homologous with the shell (van der Spoel 1976). The wings are fused together to form a large muscular wingplate (Fig. 16.64A) and the footlobes are modified into a proboscis. Cymbuliids are the largest thecosomes, reaching a maximum wingplate diameter of 80 mm in *Corolla* (Fig. 16.64A).

The viscera are situated ventrally beneath the wingplate, and are concentrated into a mass surrounded by the mantle. The heart and kidney are dorsal to this visceral mass. The anus is located on the left of the mantle cavity and the penial aperture is situated dorsally. The two cephalic tentacles are symmetrical and located on the dorsal surface of the head. The gill is absent and respiratory exchange is thought to occur over the wing surface (van der Spoel 1976).

The buccal region is greatly reduced in cymbuliids. In *Cymbulia* the radular formula is 1-1-1 and the odontophore is reduced (van der Spoel 1976). In *Corolla* and *Gleba* the jaw, radula and salivary glands are absent. A chitinous gizzard and style sac are present in all cymbuliids (Howells 1936).

Food collection by pseudotheosomes was not fully understood until field observations were made by Gilmer (1974). In *Cymbulia* the sheet-like mucous feeding web can reach up to 2 m in diameter. The web is secreted by mucous glands on the periphery of the wingplate. In this group, unlike euthecosomes, the proboscis is used to collect food particles off the web; they are then directed towards the mouth (Gilmer 1974). *Corolla* species also have a free-floating mucous web (Gilmer 1972).

Cymbuliids make use of whatever planktonic food is available. Their prey is limited by the dimensions of the ciliated grooves through which the food must pass to enter the funnel-shaped mouth. Prey items include diatoms, flagellates, heteropods, copepods and chaetognaths (Howells 1936; Thiriot-Quievreux 1970). With the wingplate extended and their sheet-like mucous web set, these molluscs can float successfully (Gilmer 1974). They are generally slower swimmers than euthecosomes and they employ the edges of the wingplate in a sculling motion when swimming. The animal can escape predation by releasing its web and swimming away at speeds up to 0.45 m/sec (Gilmer & Harbison 1986). According to van der Spoel (1976), the loss of a real shell shows that these pseudotheosomes are more completely adapted to a floating planktonic life than are euthecosomes.

Cymbuliids are protandric hermaphrodites but little is known about their reproductive biology. The reproductive system is similar to that of euthecosomes. Eggs are spawned in mucous strings or in bundles (Lalli & Gilmer 1989). Veligers have a bilobed velum and a sinistral limacinid-like shell which is cast off at metamorphosis. The velum develops into four lobes and eventually into eight lobes prior to metamorphosis. The wings start to develop and the shell is cast off when the body reaches 2.1 mm in diameter (Thiriot-Quievreux 1970; van der Spoel 1976).

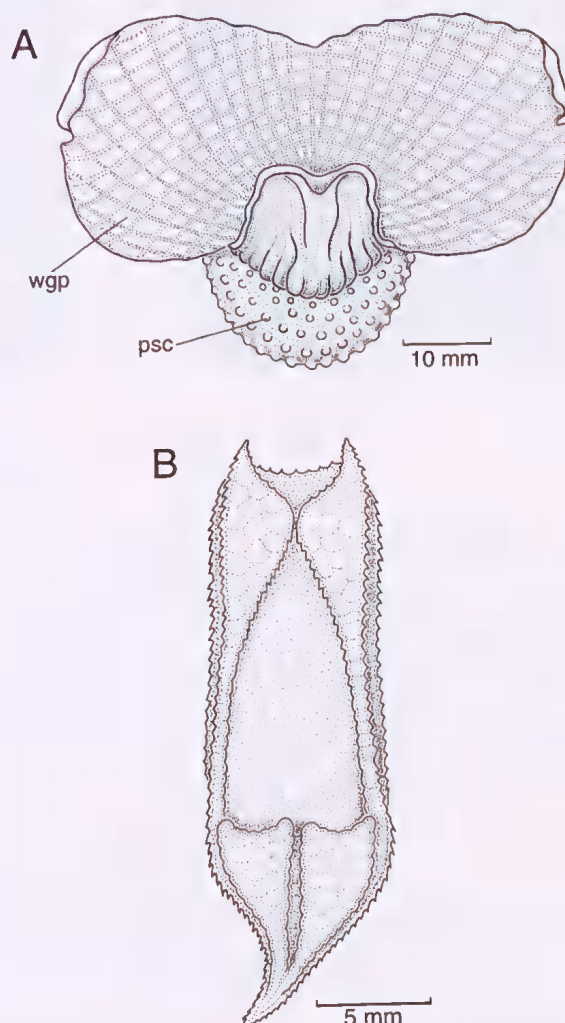


Figure 16.64 Family Cymbuliidae. A, *Corolla ovata*, animal and pseudoconch. B, *Cymbulia sibogae*, pseudoconch, ventral view. psc, pseudoconch; wgp, wing plate. [L. Newman]

Only three cymbuliid species are known from Australian waters. *Cymbulia sibogae* and *Corolla intermedia* are commonly found in tropical waters off northern Western Australia and *Corolla ovata* is common in the Gulf of Carpentaria (van der Spoel 1976; Newman 1990). The genus *Gleba* is not recorded from Australian waters (Tesch 1948). Because of their relatively large size, these pteropods may escape capture by net avoidance. Except for feeding studies, virtually nothing is known about the ecology of these molluscs.

Species identification is based on the shape and sculpturing of the pseudoconch. *Cymbulia* species have a slender, narrow pseudoconch which is ornamented with small spines (Fig. 16.64B). The pseudoconch in *Corolla* is rounded and covered in a regular pattern of round pustules (Fig. 16.64A). Species can also be differentiated on the shape of the wingplate and length of the proboscis if the animal is found detached from its pseudoconch. The wingplate is conspicuous in plankton samples due to its relatively large size and muscle band pattern. The completely transparent pseudoconch is usually detached and is virtually impossible to see in liquid; only decantation of a sample will locate these structures needed for identification. Ultimately, the best method of study is *in situ* observation and hand collection so that the animal and its pseudoconch can be collected undamaged. The feeding biology of cymbuliids is described by Lalli & Gilmer (1989) and their taxonomy and biogeography are reviewed by van der Spoel (1976).

Family Desmopteridae

Unlike other thecosomes, members of this family do not have a shell, pseudoconch, proboscis or mantle cavity. Desmopterids are rare in Australian waters, and extremely small; total body length is less than 2 mm although the wingplate can reach 5 mm in diameter.

In 1889, Chun placed the desmopterids within the Gymnosomata due to the absence of a shell. In the same year, Pelseneer placed the genus within the Thecosomata (family Cymbuliidae). Meisenheimer (1904) elevated the genus to a separate family where it remains today, and according to van der Spoel (1976) the family occupies an aberrant systematic position. Virtually nothing is known about desmopterid ecology or life history.

The wingplate is the most conspicuous part of these thecosomes. Bright red spots cover the wingplate and body (Essenberg 1919). The body is held perpendicular to the wingplate and its anterior border is indented to form five lobes with two epipodial tentacles on each side. These tentacles are probably sensory, responding to touch. Since the animals have a comparatively large wingplate, their swimming action is probably a slow sculling movement like that of other pseudotheosome families.

The buccal mass and radula are well developed. The mantle cavity is absent and the foot parts are reduced. According to van der Spoel (1976), a gizzard is absent and the digestive gland is formed from the stomach wall. The mucus-secreting pallial glands are also absent and Lalli & Gilmer (1989) surmised that these pseudotheosomes probably do not feed with a mucous web. The food and feeding behaviour of these animals are unknown.

Desmopterids are well represented throughout the subtropical and tropical Atlantic and Pacific Oceans. The family includes the single genus *Desmopterus* and three known species, differentiated solely on the length of the two epipodial wing tentacles (van der Spoel 1976). According to van der Spoel, *D. gardineri* is restricted in distribution to the west coast of Australia. *D. papilio* (Fig. 16.65) has been found commonly in the Gulf of Carpentaria, but rarely on the east coast of Australia (Newman 1990). Van der Spoel's (1976) review of the Pseudotheosomata is the most comprehensive work on these unusual opisthobranchs.

Order GYMNOSOMATA

Morton (1958a) considered the opisthobranch orders formerly grouped as pteropods (Thecosomata and Gymnosomata) to be distinct in every regard, with the exception of their swimming

mode. In the Gymnosomata (gymnosomes), the shell, mantle and mantle cavity are lost in the adult stages. These streamlined, naked pteropods are bilaterally symmetrical and the body is clearly divided into a head and a trunk which tapers posteriorly. The buccal appendages are complex and adapted for predation, mainly on thecosomes.

Huxley (1853) placed gymnosomes within the Cephalopoda due to the presence of acetabuliferous (suckered) arms; however, these buccal appendages are found only in one family, the Pneumodermatidae (Fig. 16.66). Cephalopods and gymnosomes are the only molluscs with suckers on the tentacles or buccal arms.

The first gymnosome known to science was that figured by Martins in 1676, now known as *Clione limacina* (cited in Chen 1962). Studies on the ecology, behaviour and life history of gymnosomes are few and deal mainly with *C. limacina* which is common circumglobally in Arctic and Antarctic waters. Details of the anatomy, morphology and biology of *C. limacina* were reviewed by Lalli (1970a).

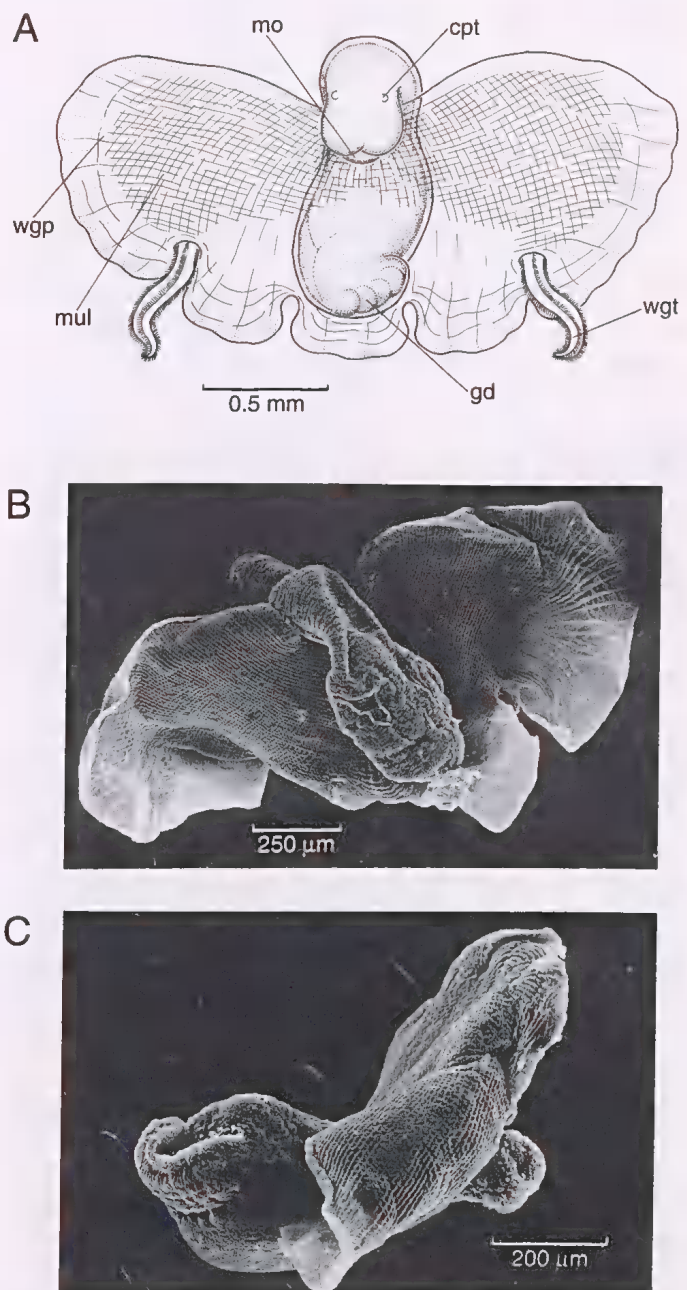


Figure 16.65 Family Desmopteridae. *Desmopterus papilio*: A, B, animal, ventral views; C, animal, lateral view. cpt, cephalic tentacle; gd, gonads; mo, mouth; mul, muscle bands; wgp, wing plate; wgt, wing tentacle.

[L. Newman]

16. OPISTHOBRANCHIA

The footlobes (one median and two lateral) are considered to be homologous with the molluscan foot and are situated between the wings. Gymnosomes are commonly known as sea-angels because of their slender body shape and synchronised wing motion when swimming. The wings are employed in a sculling action and the animals can attain a rapid speed in pursuit of their prey or to avoid predators.

The gills, if present, are situated on the right side and/or at the posterior end of the trunk. The gills are most pronounced in the family Pneumodermatidae where the posterior gill may be elaborately fringed, thereby increasing its surface area (Lalli 1970b). The function of these gills is not clear as there is no vascularisation (van der Spoel 1976).

The buccal apparatus may consist of a radula, proboscis, hook sacs and either cephaloconi (buccal cones) or acetabuliferous arms which can be evaginated during feeding. The buccal arms grab and hold the prey while the hooks are everted and used to pull the prey into the mouth. The proboscis is eversible and the radula, situated distally, is used to tear and macerate the tissue. The radular formula is variable but most species have a central tooth bordered by one to 15 long, curved, lateral and marginal teeth. The hook sacs are situated on each side of the radula and may have as many as 100 hooks per sac. The feeding efficiency of gymnosomes is considered to equal that of cephalopods and chaetognaths (Morton 1958a).

Sense organs include three labial or anterior tentacles, paired posterior tentacles with rudimentary eyes, rhinophores, an osphradium and statocysts. The rhinophores surround the base of the eyes and the unpaired osphradium is found next to the anus on the right ventral surface, below the footlobes (van der Spoel 1964). There are five pairs of ganglia, four of which form the circum-oesophageal nerve ring; the fifth pair form the buccal ganglia.

Gymnosomes are simultaneous hermaphrodites at maturity (Lalli & Gilmer 1989), rather than protandric like thecosomes. The ovotestis is located posteriorly to the visceral mass and the genital opening is situated on the right side below the wing. During copulation, the pair attaches ventrally. Fertilisation is reciprocal; the penis from each animal is inserted in the genital aperture of the partner.

Eggs are deposited in round or oblong floating egg masses, which are formed with the aid of the footlobes. Veliger larvae hatch from the eggs in a few days and have a bilobed velum and thimble-shaped shell. The shell is cast off upon metamorphosis to the second gymnosome larval stage, the polytrochous larva. Characteristically, these larvae have three ciliary bands which are used in locomotion until the wings are fully developed (Fig. 16.66E; Lalli & Conover 1976; van der Spoel 1976; Newman & Greenwood 1988). Van der Spoel & Diester-Haass (1976) reported fossil gymnosome larval shells.

Some 50 gymnosome species are known from the world's oceans. Gymnosomes are solitary by nature compared with the more abundant and sometimes swarming thecosomes (shelled pteropods). The majority of species are epipelagic and cosmopolitan, and are found commonly in tropical and subtropical seas. Tesch (1950) believed that gymnosomes are generally rare, with the exception of *Clione limacina* and *Hydromyles globulosa*, which frequently occur in large numbers.

In Australian waters, gymnosomes are uncommon in comparison with thecosomes and heteropods. Only *Hydromyles globulosa* is found in large numbers (Newman 1990). Tesch (1950) reported only four species in Australian waters and Russell & Coleman (1935) found only two species within the Great Barrier Reef. Newman (1990) subsequently added eight new records and extended species ranges. Two new pneumodermatid species have also been described from the waters of the Great Barrier Reef (Newman & Greenwood 1988; Newman & van der Spoel 1989).

Five gymnosome families are treated here, in two separate groups. The Gymnosomata includes the four families, Pneumodermatidae, Clionidae, Notobranchaeidae and Cliopsidae, all with the body

divided into head and trunk. The Gymnoptera comprises two families, Hydromylidae, in which the body is not divided into the two regions and the Laginiopsidae which is not included here. The single laginiopsid species, *Laginiopsis trilobata*, is described from one specimen collected from the Azores (Lalli & Gilmer 1989); little is known about it.

Discrimination at the family level is based on the presence of such features as lateral or posterior gills, buccal cones or acetabuliferous arms, and overall body shape. Species identifications are based on the arrangement of the buccal apparatus. In summarising the problem of gymnosome identification using preserved specimens, Tesch (1950) asked 'what are we to do with these unsightly, shapeless, deformed balls, contracted to the utmost, hiding gills, buccal organs and still more; radula, hook sacs and jaw, which are of the greatest systematic value.' Gymnosomes remain a poorly understood group of molluscs (Lalli & Gilmer 1989) and only by studying these animals alive in the field will their biology be fully understood.

Specimens should be hand collected, relaxed, and preserved in 3–5% buffered formalin. Gymnosome morphology and anatomy were discussed by Meisenheimer (1905), Massy (1917) and Pruvot-Fol (1924, 1942, 1954). Feeding and reproductive biology studies were reported by Lebour (1931), Morton (1958a), Lalli (1970a, 1970b) and Lalli & Gilmer (1989). Van der Spoel (1976) reviewed the taxonomy and biogeography of all gymnosomes.

Suborder GYMNOSOMATA

Family Pneumodermatidae

Pneumodermatids (Fig. 16.66; Pl. 34.2) are the only gymnosomes with acetabuliferous (suckered) buccal arms. In overall appearance, these gymnosomes are similar to the streamlined clionids, especially when the buccal arms are withdrawn. Both lateral and posterior gills may be present, although the lateral gill, situated on the right side, is generally observed only in live specimens (Lalli 1970b). Stellate chromatophores often occur on the surface of the body, and give the animal a brown or purple colour. The largest pneumodermatid, *Pneumoderma atlanticum pacificum*, can reach a body length of 25 mm (van der Spoel 1976).

The buccal apparatus of these animals usually consists of two lateral buccal arms, with or without a median buccal arm, and a long proboscis, jaw, radula and hook sacs. The suckers can be stalked and situated on the buccal arms, or attached directly to the buccal wall. The arrangement of these buccal appendages is useful for species identification. The structure of the jaw, hook sacs and radula is also species specific. Two hook sacs, situated on each side of the radula, may be simple or complex and hold as many as 100 hooks each. Similarly, the radular formula, including the number of lateral teeth and the presence or absence of a median tooth, varies intraspecifically. The proboscis, with the mouth situated distally, is evaginated only during feeding.

These gymnosomes feed on shelled thecosomes (Lalli 1970b). *Pneumodermopsis paucidens* (Fig. 16.66B, C) has been found to prey on euthecosomes, especially creseids. The prey is captured with the buccal suckers which attach to the inside of its shell aperture. The proboscis is evaginated into the shell, and the body of the prey is ingested (Sentz-Braconnot 1965; van der Spoel 1976). Lalli & Gilmer (1989) also observed individuals of *Pneumodermopsis canephora* feeding on *Diacavolinia longirostris*. Other prey include cladocerans and chaetognaths (Boas 1886; Massy 1917; Pruvot-Fol 1954; van der Spoel 1976). Russell (1960) reported pneumodermatids in the stomachs of lancet-fishes and Stock (1971, 1973) found these gymnosomes to be parasitised by copepods.

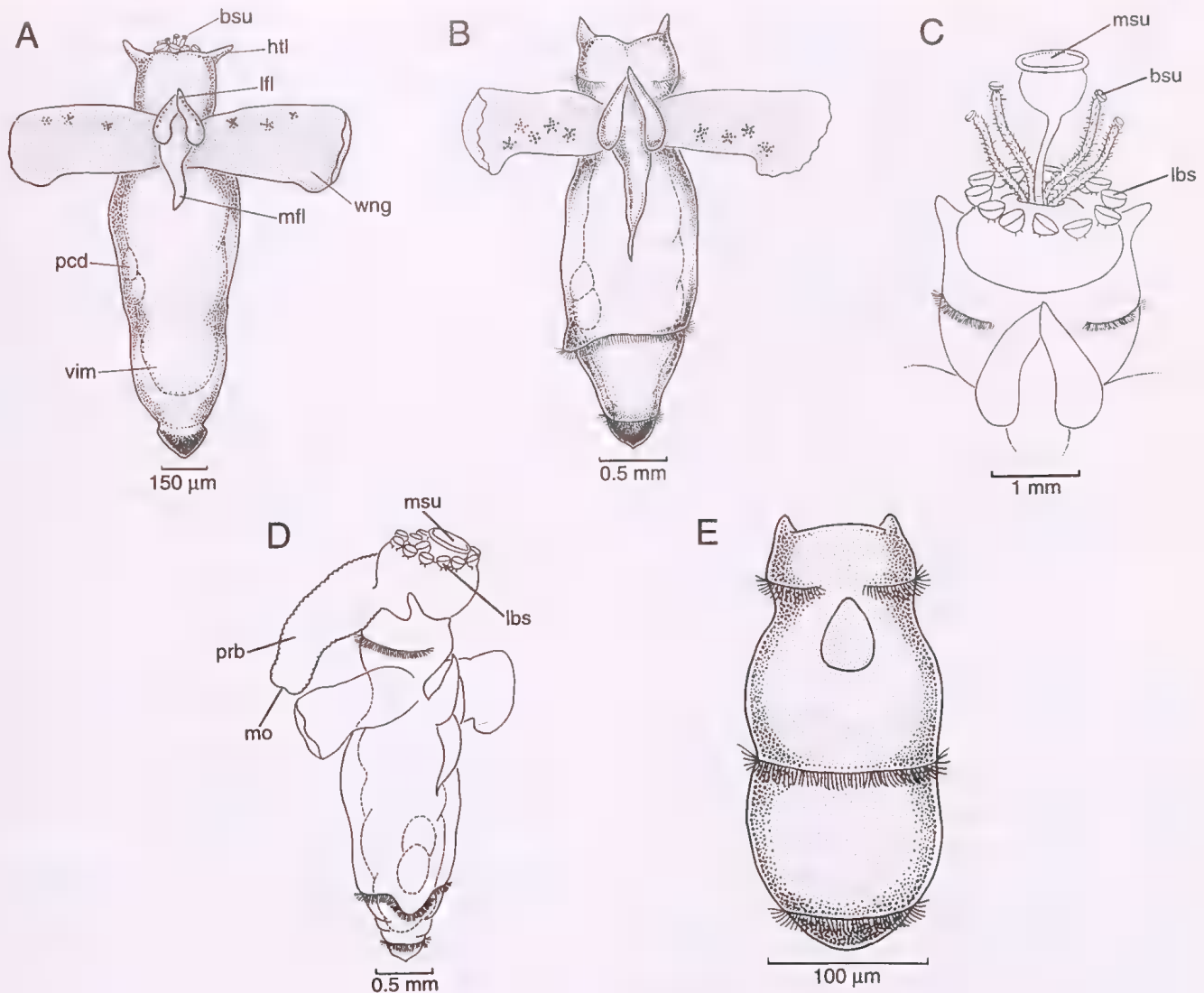


Figure 16.66 Family Pneumodermatidae. A, *Pneumodermopsis spoeli*, animal with buccal appendages evaginated, ventral view. B–D, *Pneumodermopsis paucidens*: B, animal with buccal appendages invaginated, ventral view; C, details of the evaginated acetabuliferous arms; D, animal with its proboscis extended, lateral view. E, polytrochous larva. bsu, buccal suckers of the acetabuliferous arms; htl, head tentacle; lbs, lateral buccal suckers; lfl, lateral footlobe; mfl, median footlobe; mo, mouth; msu, median sucker; pcd, pericardium; prb, proboscis; vim, visceral mass; wng, wing. (After Newman & Greenwood 1988) [L. Newman]

The family is represented by four genera *Pneumodermopsis*, *Pneumoderma* and *Spongiobranchaea* and *Schizobranchaea*. All but *Schizobranchaea* occur in Australian waters. Genera and species are distinguished by the number and arrangement of the buccal suckers and the arrangement of posterior and/or lateral gills, which can be difficult to see in preserved specimens. One genus, *Pneumoderma*, is divided into two subgenera based upon the presence (*Pneumoderma*) or absence (*Crucibranchaea*) of a median buccal arm.

Two pneumodermatid species are common in Australian waters. *Pneumoderma* (*Crucibranchaea*) *macrochira* is known from eastern Australian waters (Tesch 1950) and *Pneumoderma atlanticum atlanticum* has been reported from the North West Shelf, the Arafura Sea, the Gulf of Carpentaria and eastern coastal waters (van der Spoel 1976; Newman 1990). *Pneumoderma mediterraneum*, *P. heronensis* (Pl. 34.2), *Pneumodermopsis paucidens* (Fig. 16.66B), and *P. spoeli* (Fig. 16.66A) are found in Great Barrier Reef waters (Russell & Coleman 1935; Newman & Greenwood 1988; Newman & van der Spoel 1989; Newman 1990). *Pneumodermopsis canephora* is known only from waters off northern Western Australia (Newman 1990). *Spongiobranchaea australis* is restricted to Subantarctic waters (van der Spoel 1976).

If specimens are contracted, dissection is required for examination of the buccal appendages. Pneumodermatid taxonomy and distribution were reviewed by Tesch (1950), Pruvot-Fol (1954) and van der Spoel (1976).

Family Notobranchaeidae

This gymnosome family is represented by a single genus, *Notobranchaea*, with eight species. The body is more or less oval, but pointed posteriorly, and the head is enlarged (Fig. 16.67). The buccal apparatus consists of two pairs of cephaloconi (adhesive buccal cones) which are often reduced, and denticles are found on the outer rim of the buccal mass. The shallow hook sacs carry few hooks. The median radular tooth is unicuspidate and the number of lateral teeth can vary from two to 10. The posterior gill can be triradiate or tetradiate and fringed. The lateral gill is present as a small protrusion or is lacking. The lateral footlobes are usually ribbon-like and the median lobe is long. The maximal body length is 16 mm (van der Spoel 1976; van der Spoel & Pafort-van Iersel 1985).

The distribution of the genus *Notobranchaea* is unclear, as representative specimens are always rare. Their depth range is 100–1750 m (van der Spoel & Pafort-van Iersel 1985). Within Australian waters, *N. inopinata* is known from the Arafura Sea and off the south-eastern coast, and *Notobranchaea tetrabranchiata* is only known from a few records in the Arafura Sea (van der Spoel 1976). Studies on this family are few and virtually nothing is known of their ecology, behaviour and life-history.

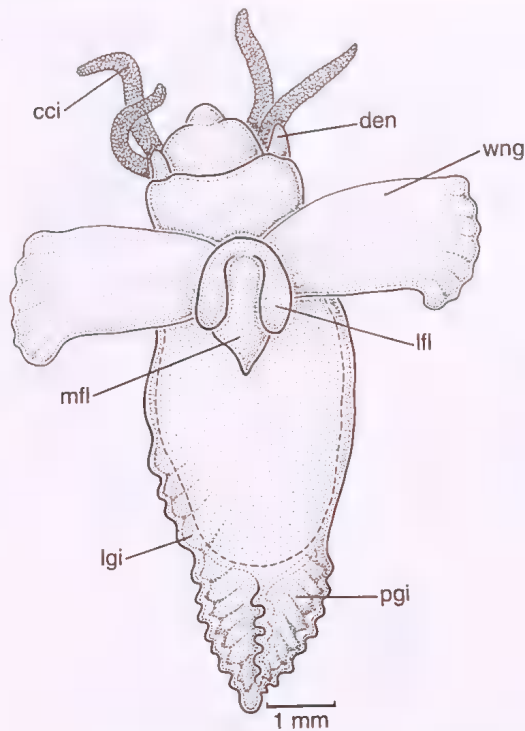


Figure 16.67 Family Notobranchaeidae. *Notobranchaea macdonaldi*, ventral view. cci, cephaloconi; den, denticle; lfi, lateral footlobe; lgi, lateral gill; mfi, median footlobe; pgi, posterior gill; wng, wing. [L. Newman]

Family Cliopsidae

Cliopsids are rarely found in Australian waters. The body is soft, gelatinous and not streamlined (Fig. 16.68). Buccal cones and acetabuliferous arms are absent. The median footlobe is reduced or lacking and the wings are relatively small. Both lateral and fringed posterior gills may be present. Cliopsids can reach 40 mm in length (van der Spoel 1976). There are only two genera in this family, *Cliopsis* and *Pruvotella*. Genera are differentiated by the presence or absence of a lateral gill.

In *Cliopsis*, the visceral mass does not fill the body cavity, giving the body an empty balloon-like appearance. Live animals are usually yellow or brown in colour. The extremely long proboscis reaches more than two times the body length when evaginated. The remaining buccal organs cannot be protruded.

The visceral mass of *Pruvotella* is distinctly red or violet in colour. Both lateral and posterior gills are present, the former encircling the body. Maximum body length is 5 mm for this genus (van der Spoel 1976).

Little is known about the ecology, behaviour or life history of these tiny gymnosomes. *Cliopsis* have been observed to feed on the pseudothecosome *Corolla*, eating the wingplate and viscera and leaving the empty pseudoconch (Lalli & Gilmer 1989).

Cliopsis krohni is the most common member of the family in Australian waters, and occurs in the Gulf of Carpentaria and off the east and north-west coasts (van der Spoel 1976; Newman 1990). *Pruvotella* is known from only one record off the coast of New South Wales (Tesch 1950). This family has been reviewed by Pruvot-Fol (1924, 1954) and van der Spoel (1976).

Family Clionidae

The family Clionidae is the only gymnosome family that has been studied in detail. Lacking external gills, these slender gymnosomes are streamlined. The body is clearly divided into a head and a trunk which tapers posteriorly (Fig. 16.69). Clionids are usually equipped with adhesive buccal cones termed cephaloconi, not the acetabuliferous buccal arms that occur in Pneumodermatidae. The largest species attains a length of 85 mm (Gilmer & Lalli 1990).

The division of the family into two subfamilies, Clioninae and Thliptodontinae, is based on the presence or absence of true cephaloconi, respectively (van der Spoel 1972). Species in the type genus, *Clione*, have six cephaloconi. The footlobes are well developed and are usually represented by one median and two lateral lobes. The body may be orange to red in colour (as in *Clione*), or covered with stellate chromatophores giving a brown-purple colour.

Morton (1958a) described the swimming mode of *Clione limacina*. The short wings are employed in a sculling motion producing a faster movement than their larger-winged thecosome prey. Clionids actively swim horizontally or vertically and sinking is accomplished by retraction of the wings.

The cephaloconi are arranged in a circle around the mouth. Each hook sac is evident as a cluster of about 100 chitinous hooks on each side of the protrusible buccal mass. The cephaloconi are extruded by the pressure of the body fluids and are retracted by muscles (van der Spoel 1976). The salivary glands are long and slender, and open at the sides of the radular sac. The radular formula can vary intraspecifically, especially with regard to the number of lateral teeth. In *Clione*, the number of lateral teeth ranges from six to 15. A long and narrow oesophagus opens into a reduced stomach and the intestine is narrow. The visceral mass does not extend to the posterior end of the trunk.

Clionids are thought to seek their prey actively. The prey, primarily shelled thecosomes, is seized with the buccal cones which position the aperture of the victim's shell over the mouth. The hook sacs are everted, and the hooks are used to pull the body out of its shell, leaving the shell empty. The radula is used to tear and macerate the soft tissue. Clionid predators include herring, mackerel, salmon, seabirds and whales (Lalli 1970a).

The circulatory system is simple. The heart is located posterior to the visceral mass. The whole body encloses a blood-filled haemocoel. The renal opening is near the anus. External gills are absent and gas exchange is thought to occur across the body surface.

The ovotestis is situated below the visceral mass. Copulation, as observed by Lalli & Conover (1973), is simultaneous as the mating pairs come together, and fertilisation is reciprocal. Gravid animals swim to the surface and, with the aid of the footlobes,

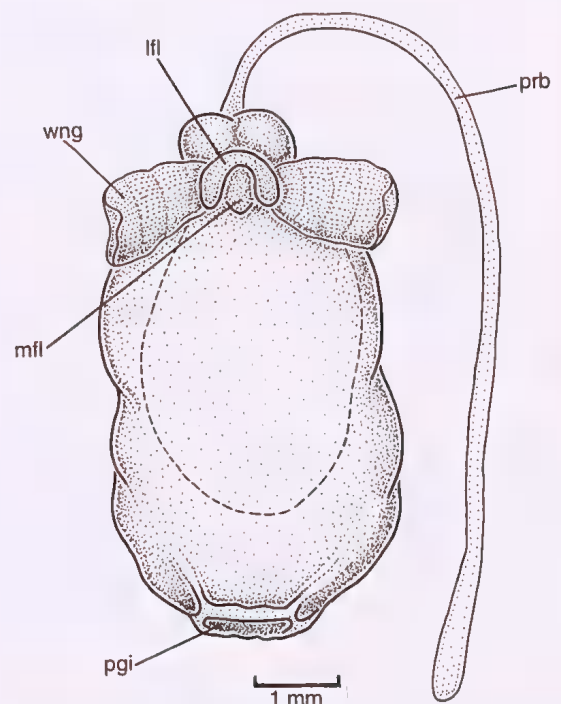


Figure 16.68 Family Cliopsidae. *Cliopsis krohni*, with evaginated proboscis, ventral view. lfi, lateral footlobe; mfi, median footlobe; pgi, posterior gill; prb, proboscis; wng, wing. [L. Newman]

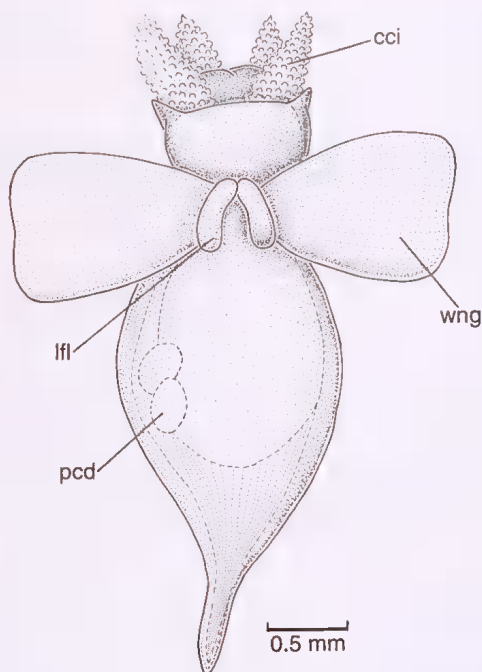


Figure 16.69 Family Clionidae. *Paraclione longicaudata*, with its adhesive cephaloconium evaginated, ventral view. cci, cephaloconium; lfl, lateral footlobe; pcd, pericardium; wng, wing. [L. Newman]

deposit a round, mucous egg mass. Veligers hatch within a few days, and have a thimble-shaped shell which is cast off when they metamorphose into polytrochous larvae. These larvae feed on limacinid thecosome veligers (Conover & Lalli 1972) and phytoplankton (Mileikovsky 1970). *Paedoclione doliiformis* has three ciliary bands in the adult stage, indicating that some clionids are neotenous (Lalli 1972).

The life histories of only two North Atlantic clionids have been studied in detail – *C. limacina* and *P. doliiformis* (Lebour 1931; Morton 1958a; Lalli 1972). Spawning patterns were found to depend on the availability of phytoplankton for the veligers and early polytrochous larvae. Breeding cycles were also found to correlate with seasonal changes in water temperature.

Only three clionid species have been found in Australian waters. *Paraclione longicaudata* is most common, occurring in warmer waters from the North West Shelf and the Gulf of Carpentaria to the north-eastern coast (Newman 1990). Rarely, a species of *Thliptodon* has been collected from off the south-eastern coast (van der Spoel 1976), and *Clione limacina antarctica* has a circum-Antarctic distribution.

Studies on the feeding, behaviour and life history of clionids were made by Morton (1958a), Lalli (1970a, 1970b, 1972), Conover & Lalli (1972), Lalli & Conover (1973) and Lalli & Gilmer (1989). The biogeography and taxonomy of clionid gymnosomes were reviewed by Tesch (1950) and van der Spoel (1976).

Suborder GYMNOPTERA

Family Hydromylidae

This family contains only one species *Hydromyles globulosa* (Fig. 16.70). It is moderately common in surface waters off eastern Australia (Newman 1990), although it is often overlooked in plankton samples because of its resemblance to a fish egg. *Hydromyles globulosa* does not resemble any other gymnosome. Little is known about its biology.

The animal is encased in a transparent and flexible shell-like cuticle, the surface of which is composed of hexagonal cells which can usually be seen through the outer integument. The internal organs are often yellow or orange in colour, except the dark green digestive gland which is visible through the cuticle.

When extended, the animal is oval in shape and the two wings, footlobes and two tentacles extend through a semi-circular, slit-like opening located antero-ventrally. When contracted and the anterior parts are withdrawn, this gymnosome is completely spherical. A fold in the cuticle seals the opening. The maximum body length is approximately 10 mm.

The two wings are tubular in shape, with paddles at their distal ends. During swimming, both wings are flapped symmetrically with the aperture directed toward the water surface.

Buccal cones, acetabuliferous arms, proboscis and hook sacs are absent in these gymnosomes. The radular formula (1-1-1) resembles that of thecosomes (Lalli & Gilmer 1989). The anterior head tentacles are also unusual in being covered by rows of cilia. Whether these tentacles are employed in food capture has not been established.

Two salivary glands empty into the buccal cavity and lie along the oesophagus. The digestive system is similar to those of other gymnosomes except that the intestine emerges on the dorsal side. A gizzard is absent. The anus is found ventrally on the right side near the genital opening (Lalli & Gilmer 1989). The feeding biology of these gymnosomes is poorly understood.

Hydromyles is the only gymnosome that is known to be ovoviviparous (Tesch 1950). The young develop in a brood chamber which is formed by the accessory reproductive gland of the female. Eventually the larvae break through the gland wall and grow in the visceral cavity. Reduction of the visceral mass occurs in the female as the embryos develop. The female becomes so full of young that her body wall atrophies and finally bursts, releasing the young veligers (van der Spoel 1976). The veligers are totally transparent, have two ciliary bands around the posterior part of the body and are approximately 1 mm in length (Newman 1990).

Van der Spoel & Heyman (1983) have reviewed the biogeography of this family. *Hydromyles globulosa* is found along the east coast of Australia from southern Victoria, north to Lizard Island. The species is known to occur in tropical and subtropical Indo-Pacific waters, but has not yet been recorded from the Gulf of Carpentaria or in the waters between northern Australia and Papua New Guinea (van der Spoel & Heyman 1983; Newman 1990). Tesch (1950), however noted that swarms of these animals (up to 3000 animals per plankton tow) occurred in surface waters throughout the Indo-Pacific. Details of the anatomy of *H. globulosa* are given by Pelseneer (1887) and Meisenheimer (1905).

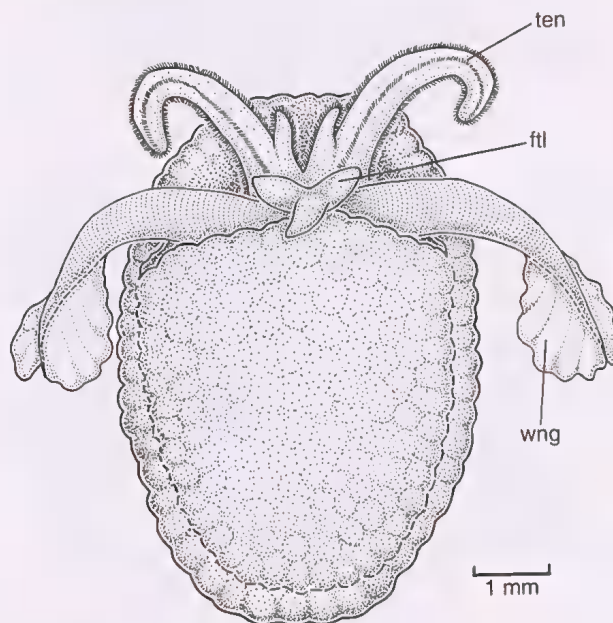


Figure 16.70 Family Hydromylidae. *Hydromyles globulosa*, with wings and buccal apparatus extended through the apertural opening, ventral view. fl, footlobe; ten, tentacle; wng, wing. [L. Newman]

Order NUDIBRANCHIA

The Nudibranchia is the largest and most varied order of opisthobranchs. No member has a shell or operculum as an adult. The respiratory organs on the dorsal surface (anatomically the mantle) consist of either a circle of gills or thin-walled papillae (called cerata), though the numerous exceptions indicate considerable evolutionary radiation. Copious mucus is produced over the whole body surface. Glands producing repugnatory substances are often present within the integument of the mantle and aeolids generally defend themselves with nematocysts derived from their cnidarian prey. The most colourful nudibranchs are aposematic, but there are many camouflaged species as well. Some species mimic other nudibranchs, cephalaspideans, bean cowries, lamellariids, flat worms or holothurians. The majority of nudibranchs are benthic, but a few highly derived species are planktonic or pelagic. All nudibranchs are carnivorous, and their diet encompasses all the major marine animal phyla except Echinodermata.

Nudibranchs are found in all the world's oceans, and are most diverse in tropical seas. The Australian fauna is estimated to contain about 700 species. The order can be divided into two groups, the first containing the dorids (suborder Doridina) with two superfamilies, Anadoridoidea (more generally known as Phanerobranchia) and Eudoridoidea (Cryptobranchia), and the second containing the ceratal-bearing members (suborders Dendronotina, Aeolidina and Arminina). Representatives of all of these higher taxa are known from Australian waters, with the greatest number of described species in the Eudoridoidea, which is to be expected since it contains the large and showy representatives. The southern half of the Australian continent has many endemic species, but the northern half has only a few endemics and these are coastal. Curiously, the Great Barrier Reef has the richest nudibranch fauna in terms of numbers of species (approximately 400), but none is endemic.

Suborder DORIDINA

This is the largest nudibranch suborder and contains a wide variety of morphological types – commonly known as 'dorids' – which range in size from a few millimetres to over 300 mm in length. Few characters are found in all members of the suborder. Most, however, have a pair of antero-dorsal chemosensory rhinophores and a group of postero-dorsal gills, usually arranged in a circle around the anus. With few exceptions, the anus opens posteriorly in the dorsal mid-line. Internally, the digestive gland is a discrete, unbranched mass, a condition termed holohepatic, and the basis of the name 'Holohepatica' previously given to this suborder. By comparison, the suborder Aeolidina, in which the digestive gland is always branched, is described as 'cladohepatic'. Examples of both conditions are found in the suborders Dendronotina and Arminina.

Traditionally, the Doridina are divided into three or four superfamilies. One of these, the Gnathodoridoidea (= Bathydoridoidea) contains a few apparently primitive species from polar waters and is not discussed here. A second, the Porodoridoidea (= Porostomata, Dendrodoridoidea or Phyllidoidea) consists of two families, Dendrodorididae and Phyllidiidae, which have lost the radula and feed suctorially. However, as discussed below, there is no evidence to suggest that this suctorial feeding is indicative of a common ancestry for these two families, both of which are considered here to belong to the superfamily Eudoridoidea. The two superfamilies represented in Australian waters, Anadoridoidea and Eudoridoidea are discussed below.

Superfamily ANADORIDOIDEA

Members of this superfamily are all specialised for feeding on particular kinds of marine invertebrates, such as bryozoans, ascidians, sponges, polychaete worms and other opisthobranchs. The wide range of food types has led to a great diversity in foregut anatomy and tooth morphology. The superfamily is also known as

the Phanerobranchia, in reference to the lack of a pocket into which the gills can retract when disturbed. Animals range in size from about 100 mm to less than 5 mm. Some species are ovate and flattened with a wide mantle skirt, and others are slender, high and elongate with the mantle skirt completely lacking.

Families placed in the Anadoridoidea include Corambidae, Goniodorididae, Onchidorididae, Polyceridae, Gymnodorididae, Aegiretidae and Vayssiireidae.

Family Corambidae

These small dorids are always associated with the encrusting bryozoan colonies on which they feed (Pl. 35.8). The mantle is elongate-ovate and somewhat convex (Fig. 16.71). The rhinophores retract into individual pockets surrounded by a sheath and the simple gills are situated in the posterior mid-line below the mantle skirt on each side of the anus. In some species the posterior mantle skirt is raised into a pallial notch in the mid-line (Farmer 1980; McDonald & Nybakken 1980).

This family, of uncertain affinity, contains relatively few species of very similar shape. All feed on species of the bryozoan genus *Membranipora*. Though three genera have been described – *Corambe*, *Doridella* (Pl. 35.8) and *Corambella* – most authors consider the latter two genera to be synonymous. The main characters separating the genera are the presence of smooth or elaborated rhinophores and the presence or absence of a raised pallial notch on the mantle skirt. At least 12 species have been described, though further studies may show that this number could be reduced to a few circumglobal species, which have accompanied the spread of their host bryozoans. If this is so, present generic characters may prove to be only of specific importance.

The broadly ovate mantle covers the rest of the body. Unique mantle glands scattered through the epithelium produce a cuticular layer over the mantle which is sloughed off at intervals as a thin transparent sheet. The head bears a pair of elongate oral tentacles. The anus opens in the posterior mid-line below the mantle skirt. A series of glands of unknown function is present at the base of the two to 12 simple gills, which are arranged on each side of the anus. The rhinophore is either a simple smooth cylindrical rod or has one or two curved plates on each side of the central rod (MacFarland 1966).

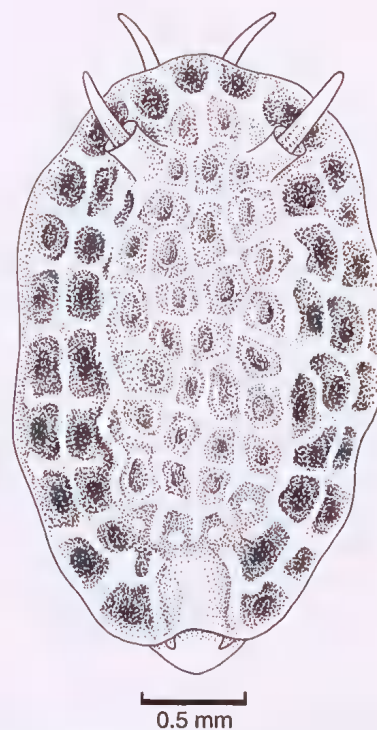


Figure 16.71 Family Corambidae. *Doridella* sp., dorsal view. (After photograph by W.B. Rudman) [S. Weidland]

The buccal bulb is lined with a chitinous cuticle which is slightly thickened at the mouth. The radula is remarkably consistent in all described species and comprises approximately 35 to 40 rows of teeth with a formula of 4-5.1.0.1.5-4. The innermost lateral tooth on each side is large and triangular with a recurved pointed cusp bearing small inner denticles. The other lateral teeth are much smaller and non-denticulate.

Corambids are clearly highly adapted to a cryptic life on encrusting bryozoans. Although the radular morphology suggests a relationship to the Goniodorididae, the retractile rhinophores do not. The position of the gills, unique amongst dorids, may be an adaptation to their cryptic life style.

The relationship of these animals to their bryozoan prey has led to a number of recent studies on their ecology and life history. All corambids feed on species of *Membranipora* (sometimes referred to subgenerically as *Electra* or *Alcyonidium*), and all are cryptically coloured, usually translucent with dark brown spots and sometimes with a white reticulate pattern matching the pattern of the bryozoan zoarium (Pl. 35.8).

Larval development and life history studies of *Doridella obscura*, from the western North Atlantic, show that it has a monthly life cycle throughout the year despite a water temperature range from 1.5–28°C (Perron & Turner 1977). Eggs hatch four days after deposition and the phytoplankton-feeding veliger larvae settle and metamorphose specifically on *Membranipora* (*Electra*) *crustulenta* after nine days. This abbreviated life cycle enables *Doridella* to take advantage of the short-lived colonies of the bryozoan (Perron & Turner 1977).

On the Pacific coast of North America, Yoshioka (1982) has shown that *D. steinbergae* (Lance 1962) and *Corambe pacifica* both induce *Membranipora membranacea* to grow spines on the zooid wall after heavy feeding, thus demonstrating that spine development is not an important diagnostic character in *Membranipora* taxonomy. Seed (1976) and Bickell & Chia (1979) provided accounts of the feeding biology of *D. steinbergae* and its larval biology.

Although there are no published records of corambid species from Australia, a species of *Doridella* is often common on *Membranipora* colonies growing on laminarian algae in south-eastern Australia.

Family Goniodorididae

These are small to medium-sized phanerobranch dorids with a greatly reduced mantle skirt (Fig. 16.72A, B). They are characterised by the shape of the radular teeth and the presence, in most species, of a large buccal pump opening into the buccal bulb. They are specialist feeders on bryozoans and compound ascidians (Baba 1960; Macnae 1958). The major genera are *Goniodoris*, *Hopkinsia* (Pl. 35.6), *Okenia* and *Trapania*. An alternative family name applied to this group is Okeniidae.

Goniodorids are small, soft animals seldom more than 20 mm long although the European *Okenia elegans* may reach 80 mm. The long, tapering rhinophores bear a few reduced lamellae and, although contractile, lack a sheath or pocket into which they can retract. Similarly the simple gills are contractile, but there is no common gill cavity into which they can retract (Thompson & Brown 1984). The gills are arranged in a circle, open posteriorly, around the anal papilla in the posterior dorsal mid-line.

The head has an oral veil which forms a pair of flattened lateral lobes in some genera and a pair of long tentacles in others. The mantle skirt is very reduced and often consists of a lateral ridge with or without a few tentacular processes. Some genera have a mid-dorsal ridge; in others, there are short or long papillae over the dorsum. The mantle skirt is reduced, and thus the foot is larger than the dorsum; it usually tapers to a rounded point posteriorly.

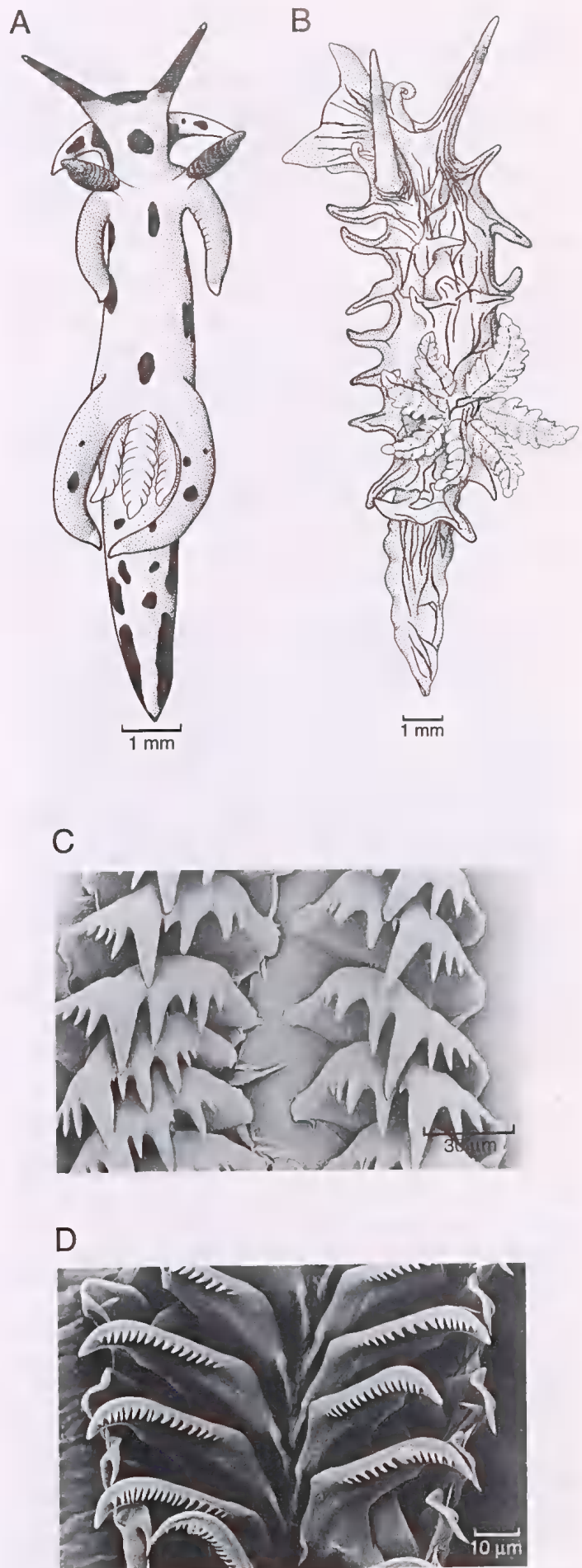


Figure 16.72 Family Goniodorididae. A, *Trapania japonica*, dorsal view. B, *Okenia pellucida*, dorsal view. C, section of radula of *Trapania japonica*. D, section of radula of *Okenia pellucida*. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C, D, G. Avern]

16. OPISTHOBRANCHIA

Jaws are not well developed and when present usually consist of a chitinous plate on each side of the mouth made up of small rod-like elements. A muscular sac, often large and sometimes pedunculate, opens off the dorsal mid-line of the buccal bulb. Known as the 'buccal pump', it apparently is used to suck food particles into the mouth. Variations of the radular formula are: 1.0.1, 1.1.0.1.1 and 1.1.1.1.1. When present, the central tooth is a very reduced plate and the outer lateral tooth, although often denticulate, is much smaller than the inner lateral teeth. The latter are large, often triangular, plates with a prominent, recurved cusp which is denticulate along its inner edge (Figs 16.10A, 16.72C, D).

Species of *Goniodoris* typically feed on compound ascidian colonies as adults and are often found nestled in cavities they have eaten out of the ascidian colony. Thompson & Brown (1984) report that juveniles of *G. nodosa* in Britain feed on encrusting bryozoans before moving to ascidians as adults. An unidentified species of *Goniodoris* and *Goniodoridella savignyi* have been found feeding on arborescent bryozoans in eastern Australia (W.B. Rudman personal observation). Species of *Hopkinsia* and *Okenia* are well-known as predators, each adapted to feeding on one or a very few species of encrusting and arborescent bryozoans. Many species show remarkable adaptations in colour and shape which camouflage them when on their prey. *Trapania*, recently reviewed by Rudman (1987c), is one genus for which food requirements and other aspects of basic biology are unknown.

Although information is available on the life history of some European species (Thompson & Brown 1984), little is known about the Australian species. The preferred food of goniodorids – colonial ascidians and bryozoans which often foul, or used to foul, the bottoms of ships – have made them ideal candidates for artificial dispersal worldwide. One species, *Okenia plana*, originally described from Japan, has since been recorded from California, eastern Australia and northern New Zealand, always on the cosmopolitan bryozoan *Membranipora* on which it feeds. Another species, *Okenia pellucida*, which is always found on the bryozoan *Zoobotryon pellucidum*, was originally described from Sydney Harbour (Burn 1967a) and is now reported from many harbours ranging from Moreton Bay, Queensland, across southern Australia to Fremantle, Western Australia, and also Auckland, New Zealand.

An eastern Australian *Goniodoris* species which feeds on ascidians is probably identical to *Goniodoris castanea*, originally described from European waters and later reported from Suez, Japan, New Zealand (Thompson & Brown 1984) and more recently South Africa (Gosliner 1987a).

Family Onchidorididae

These small to medium-sized phanerobranch dorids usually have a broad, ovate and spiculate mantle (Fig. 16.73A). They are characterised by the radular morphology and the presence of a large buccal pump opening off the dorsal side of the buccal bulb. Most species are specialised bryozoan feeders (Thompson & Brown 1984). The family is also known as the Lamellidorididae or Pseudodorididae.

The major genera are *Onchidoris*, *Adalaria*, *Acanthodoris* and *Diaphorodoris*. Species of *Onchidoris* and *Acanthodoris* are reported from south-eastern Australia (Bergh 1905b; Burn 1958, 1969) and there are unpublished records of a species of *Diaphorodoris* from Tasmania and Victoria.

The ovate mantle usually covers the depressed body completely, except in *Diaphorodoris* where the mantle skirt is somewhat reduced and the posterior foot extends some distance beyond the mantle (Millen 1985). The mantle is usually thick and verrucose or papillate. Spicules are usually present, embedded in the mantle. The rhinophores are lamellate and can retract into shallow pockets. The simple pinnate gills form a circle around the anus in the postero-dorsal mid-line. In *Onchidoris* and *Adalaria*, the vessel from each gill is inserted independently into the sub-epithelial branchial vessel. Those of *Acanthodoris* are joined

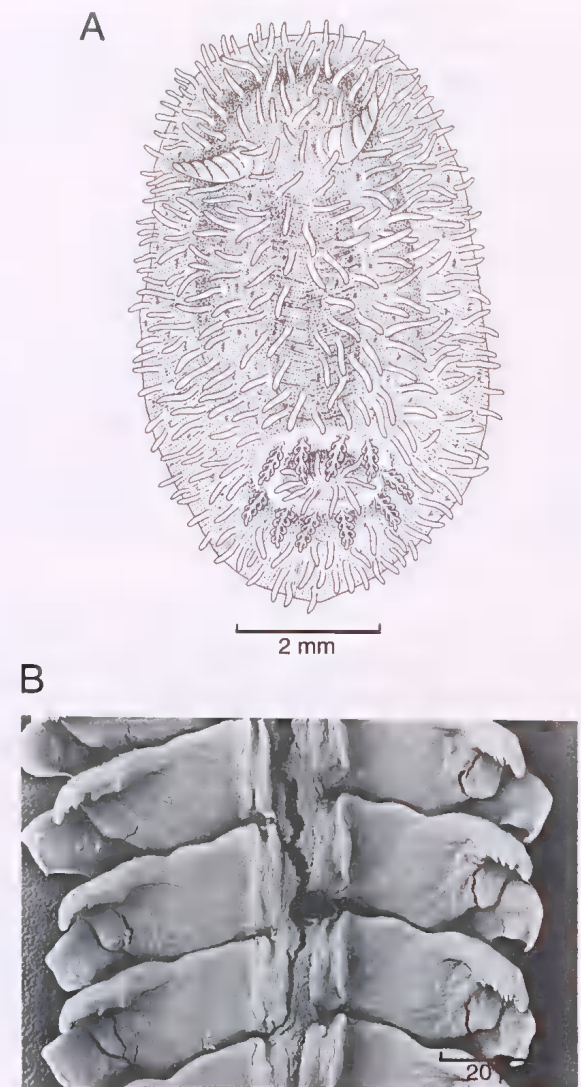


Figure 16.73 Family Onchidorididae. *Onchidoris depressa*: A, animal, dorsal view; B, section of radula. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Averm]

at their bases and the individual pits into which each gill can partially retract are interconnected (Williams & Gosliner 1979). The common pit present in *Diaphorodoris* is not sufficiently large for complete gill retraction.

A rounded velum on the head may be bilobed or produced laterally into a pair of tentacles. The buccal cavity is lined with chitin and usually some thickening of the jaw develops. A muscular buccal pump opens off the buccal bulb. The radular teeth are fairly uniform throughout the family with the generalised formula: (13-2).1.(0-1).1.(2-13) (Fig. 16.73B). A central tooth is usually absent but a few species of *Onchidoris* and *Adalaria* have a small central plate. The innermost lateral tooth on each side is large, usually with a triangular base, and bears a large, recurved denticulate cusp. The other lateral teeth are much smaller. Sometimes these have a single cusp, or rarely a few, but most often they are simple quadrangular plates.

Nothing is known of the ecology and life history of Australian species, though such information is well known for many Northern Hemisphere species. All but one species for which information is available, feed on encrusting bryozoans. The exception, the North Atlantic species *Onchidoris bilamellata*, feeds on the barnacles *Balanus* and *Elminius*. Most species have annual life cycles. Ecological studies of European species are reviewed in Thompson & Brown (1984).

Most genera have been recorded from polar and temperate regions in both hemispheres but only a few species have been reported from the Southern Hemisphere.

Family Polyceridae

These elongate, limaciform dorids have smooth or papillate bodies and a greatly reduced mantle skirt, usually consisting only of a veil around the head and sometimes a ridge along the sides of the body. The lamellate rhinophores have a pocket, and sometimes a sheath, into which they can contract, but the gills do not. Little is known of the biology of the monotypic Kalinginae but the Triophinae and Polycerinae eat bryozoans and the Nembrothinae feed on bryozoans, ascidians and nudibranchs (Macnae 1958; Odhner 1941).

The family name (= Polyceratidae, Euphuridae) was first used by Alder & Hancock (1855) to include all the dorid genera with non-retractile gills. Bergh (1879, 1880, 1883) divided the family into those genera with a suctorial crop (Goniadorididae) and those without (Polyceridae). The relationships of these genera are still not clearly understood but many authors now restrict the Polyceridae to a few allied genera (Odhner 1941) and consider Notodorididae, Triophidae, Nembrothidae and Gymnodorididae as distinct families. In reviewing Australian species, Burn (1967b) suggested that the family should comprise the four subfamilies Kalinginae, Triophinae, Polycerinae and Nembrothinae, and that notodorids and gymnodorids should be in separate families. In the absence of any clear resolution of this problem, Burn's suggestions have been adopted here. Because of the differences between them, these four subfamilies are treated separately below.

Subfamily Polycerinae

Polycerine nudibranchs are elongate and limaciform, and attain lengths of 5–70 mm (Fig. 16.74A, B). The body is usually high and a frontal veil is the sole remnant of the mantle skirt. It may or may not bear simple tentacular processes on its edge. Along the sides of the body the mantle skirt is reduced to a few tentacular papillae, sometimes connected by a small ridge. If a ridge is present, it joins in the mid-line just behind the centrally placed gills, and may form a slight median ridge down the tapering posterior end of the combined body and foot. The rhinophores are lamellate and a rhinophoral sheath is usually lacking although it is present in some genera. The gills, usually simply tripinnate, are reduced in number and are arranged either in a circle, an arch, or in a simple row.

The buccal bulb lacks a buccal pump and has large chitinous jaws often with a wing-like accessory process. The radular formula is 2-8.2.0.2.2-8; the two innermost lateral teeth on each side are usually large, bicuspidate, hooked plates (the second being the largest), and the outer teeth are much smaller acuspidate plates (Fig. 16.74C, D). The penis is usually armed with spines.

In Australia two genera occur: *Polycera* (Fig. 16.74A), (with junior synonyms *Palio* and *Greilada*), and *Thecacera* (Fig. 16.74B).

As mentioned above the edge of the dorsum at the anterior end is produced into a rounded veil, often with a few marginal papillae. In *Polycera* there are often a few large papillae beside the gills. In *Thecacera* there is no anterior veil and each rhinophore has a large but partial sheath, opening posteriorly.

All polycerines feed on encrusting or erect bryozoans. Several polycerines recorded from Australia have a cosmopolitan distribution no doubt associated with their relationship with bryozoan colonies, which are well known fouling organisms. *Polycera capensis* was originally described from Cape Town, South Africa, but is commonly found on bryozoan colonies in Sydney Harbour, Port Hacking and Botany Bay. Dakin (1952) reported densities of 120 to 150 per m² on *Bugula* growing on the hull of a small boat. *Polycera hedgpethi*, originally described from California, is now known from South Africa, the east coast of Australia and New Zealand. *Thecacera pennigera* has perhaps the widest distribution. Originally described from England, it is well known from the North Sea and the Mediterranean, South Africa, Pakistan, Japan, Brazil, northern New Zealand and the east coast of Australia (Willan 1976). The original home of all

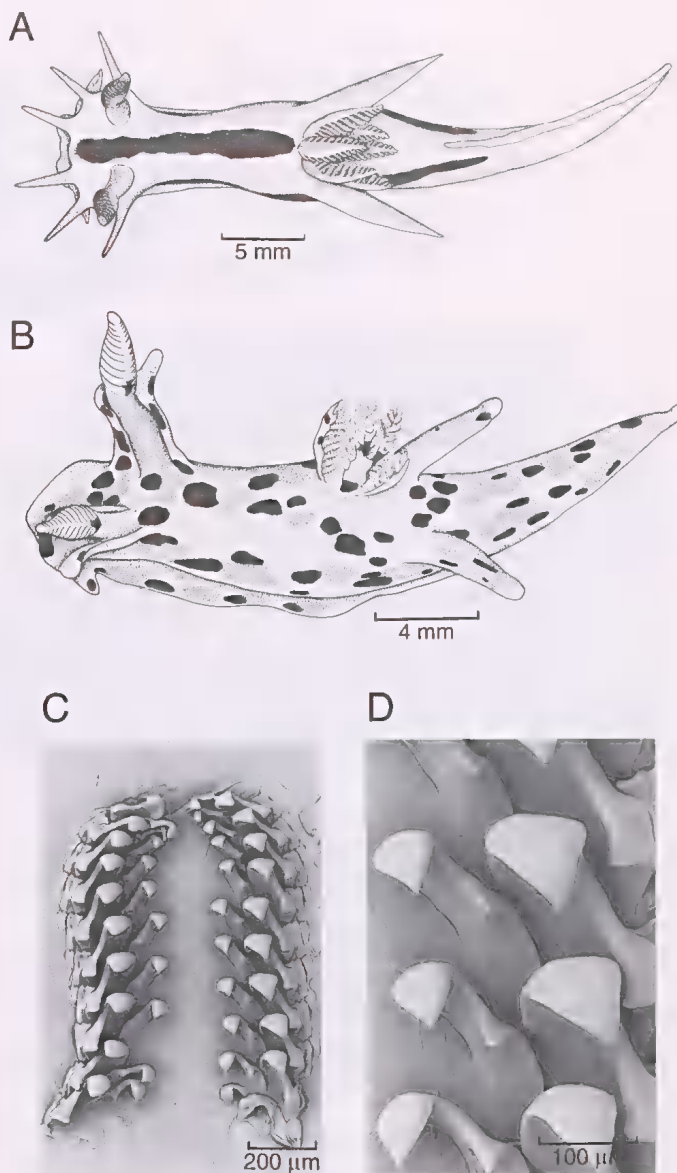


Figure 16.74 Family Polyceridae, subfamily Polycerinae. A, *Polycera capensis*, dorsal view. B, *Thecacera pennigera*, dorsal view. C, whole radula and D, section of right side of radula of *Thecacera pacifica*. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C, D, G. Averm]

these species will be difficult to determine. In Port Hacking, Sydney, all three species have been found together on the bryozoan *Scrupocellaria* cf. *scrupea*.

No ecological studies on Australian species have been undertaken, but it is probable that life cycles are rapid and opportunistic, as with other feeders on short-lived bryozoans. Studies on European species are summarised by Thompson & Brown (1984).

Subfamily Triophinae

These phanerobranch dorids have a very reduced mantle skirt, which usually consists of a veil around the head and a narrow ridge along the sides of the body (Fig. 16.75A; Pl. 35.7). The edge of the veil and the ridge usually have prominent tubercles which are often branched or papillate. The gills are bipinnate or tripinnate and contractile but lack a pocket for purposes of retraction. The lamellate rhinophores have low sheaths and are able to retract into a pocket. The oral tentacles on each side of the mouth are developed into long, wide, ridge-like lappets (Macnae 1958).

The taxonomic confusion surrounding this and related subfamilies is discussed under the Polyceridae. The typical genus *Triopha* is known only from the North Pacific. In Australian waters the common genera are *Plocamopherus* (Pl. 35.7), *Kaloplocamus* (Fig. 16.75A), *Crimora* and *Limacia*.

16. OPISTHOBRANCHIA

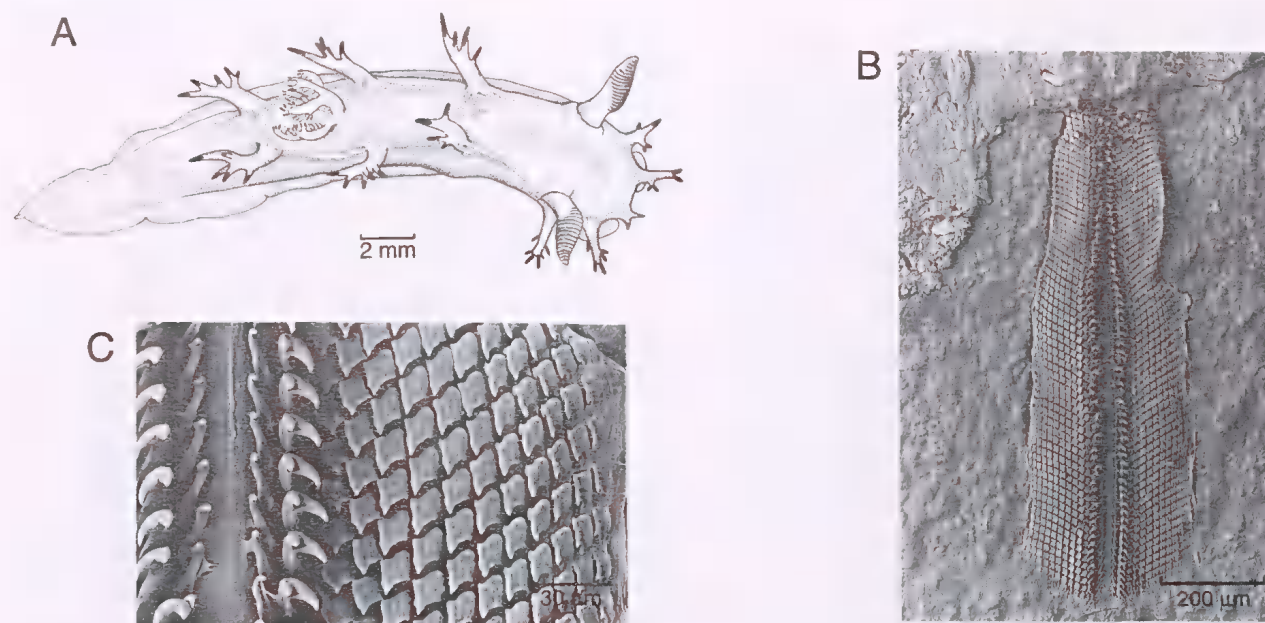


Figure 16.75 Family Polyceridae, subfamily Triophinae. A, *Kaloplocamus acutus*, dorsal view. B, whole radula and C, section of right side of radula of *Limacia ornata*. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, C, G. Avern]

The mantle edge and the dorsum and sides of the body of *Crimora* bear small pointed tubercles. There are only three gills. The radular teeth are highly differentiated. The first lateral tooth is small, the second is large, bicuspidate and like that of a polycerid, and the remaining eight to nine inner lateral teeth form interlocking pointed plates. The outer 10 teeth are long, slender, recurved and denticulate. The radula of *Limacia* is very similar (Fig. 16.75B, C) but lacks the narrow outer teeth. In *Plocamopherus* and *Kaloplocamus*, there may be three to four large, bicuspidate inner lateral teeth and up to 15 small outer plates. The radula in these two genera is characterised by a wide central region with a regular tuberculate chitinous plate of unknown function.

Triophines all apparently feed on encrusting and arborescent bryozoans. Some species of *Plocamopherus* and *Kaloplocamus* are able to swim, or at least propel themselves through the water for short periods by lateral flexion of the body. The posterior end of the foot has a long median crest which is able to be greatly enlarged dorso-ventrally when required to act as a lateral 'paddle' in swimming. Species of both genera are able to produce flashes of light when disturbed. *Plocamopherus* has large terminal swellings on some of its lateral papillae which have been described as light organs. However, when disturbed other parts of the body as well as the 'light organs' give luminescent flashes and *Kaloplocamus*, which lacks these swellings, also luminesces (W.B. Rudman personal observation). It is not known whether this luminescence is caused directly by the nudibranch or indirectly by bacteria in a symbiotic relationship.

Subfamily Nembrothinae

These are elongate, limaciform dorids in which the mantle skirt is reduced to a slight ridge around the anterior end of the body (Fig. 16.76A). The non-retractile gills form a prominent cluster about midway down the body. On each side of the mouth the oral tentacles are developed into either wide oral lappets or tubular projections. A sunken sensory pit is usually present on the side of the head below each rhinophore.

The taxonomy of this group was reviewed by Burn (1967b). His division of the 22 species then described has been accepted generally by later workers who have described at least another 10 species. The three genera, *Nembrotha* (Pl. 37.4), *Roboastra* and *Tambja* are distinguished by differences in the morphology of the radula (Fig. 16.76B–D) and the prostate gland. Unlike other polycerids, these genera have a distinct central or rachidian tooth.

The large first lateral tooth is sometimes deeply bicuspidate, and the small outer lateral plates, ranging in number from three to 10 in different genera, are characteristic of the family.

All three genera occur in Australia and some species of *Tambja* are relatively common. Those species of *Tambja* for which information is available feed on arborescent bryozoans, such as *Bugula*, and they are normally found on their food. Though feeding records for *Nembrotha* species are few, it appears that they are specific predators on colonial ascidians. There are records of American species of *Roboastra* which actively hunt and feed on species of *Tambja*, but no information is available for Indo-West Pacific species (Farmer 1978).

Subfamily Kalinginae

The single species in this group, *Kalinga ornata*, is large, up to 150 mm long (Fig. 16.77A). The mantle skirt is very reduced. It bears many large papillate processes around its narrow anterior portion, and is further reduced along the sides of the body to a ridge bearing a few large tuberculate processes with arborescent tips (Alder & Hancock 1864). The rest of the body is covered in simple and pustulose tubercles. The lamellate rhinophores are retractile. There are five to six large tripinnate gills. They form a circle around the anal papilla but each gill is inserted separately; there are no pockets into which they can retract.

The foregut is extremely large. The radula consists of rows of large tricuspidate teeth all of similar size and shape, with the formula of 135.1.135 (Fig. 16.77B). Nothing is known of the ecology or life history of this species. It is recorded from subtidal localities throughout the Indo-West Pacific from southern Africa to Japan and eastern Australia (Baba 1955; Thompson 1975).

Family Gymnodorididae

These small to large, limaciform nudibranchs have non-retractile rhinophores and gills. The mantle skirt is absent except for a small ridge around the anterior end of the body. Most species have small tubercles which are also found on the edge of the anterior mantle ridge. The gills are usually small and simply pinnate, arranged in a circle or an arc around the anus (Fig. 16.78A), or anterior to it in a line.

Most of some 20 named species from the Indo-West Pacific are considered to belong to a single genus *Gymnodoris*. The relationship of this genus with *Angasiella* and *Paliolla*, both

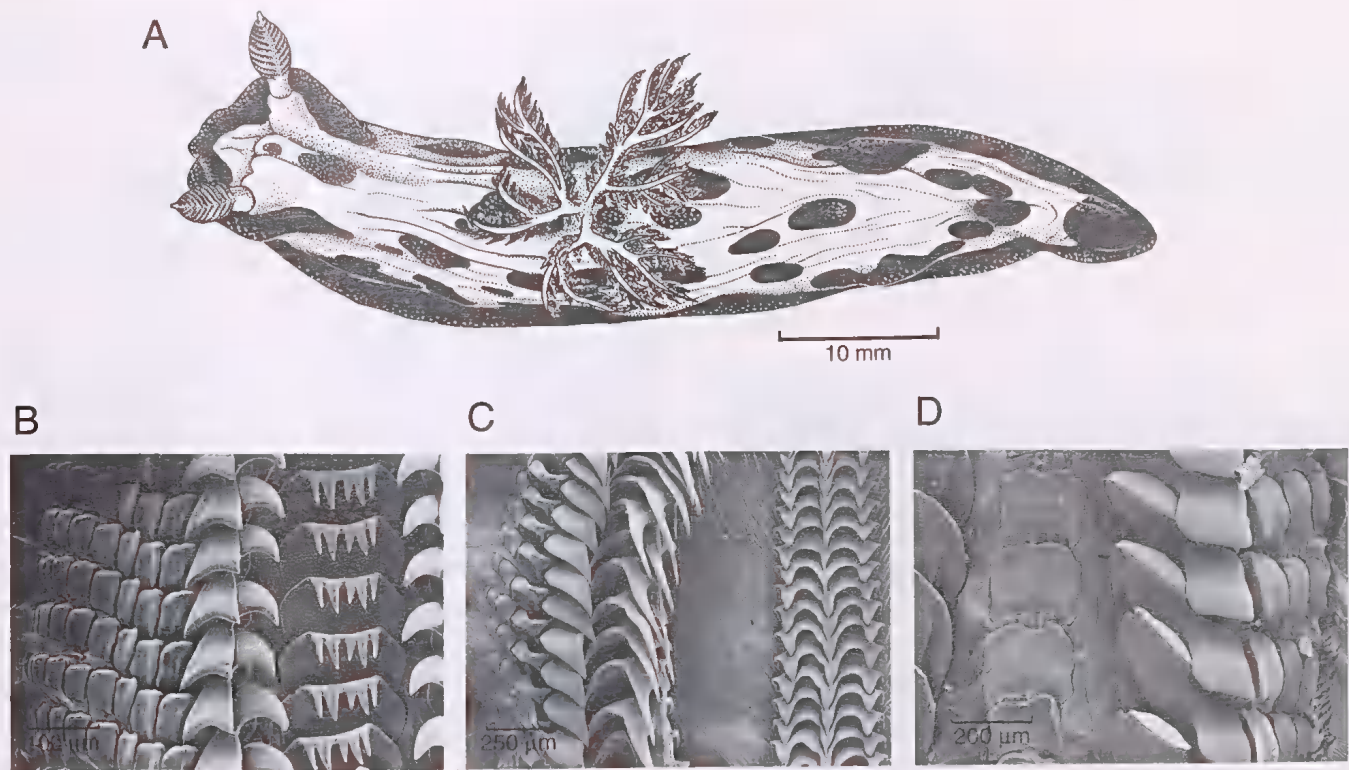


Figure 16.76 Family Polyceridae, subfamily Nembrothinae. A, *Tambja verconis*, dorsal view. B–D, radula sections: B, *Nembrotha* sp.; C, *Roboastra* sp.; D, *Tambja morosa*. (A, after photograph by W.B. Rudman) [A, S. Weidland; B–D, G. Avern]

known only from Australia, and *Lecithophorus*, which are sometimes associated with *Gymnodoris*, is not clear. The relationship of *Gymnodoris* with the subfamilies of the Polyceridae is also unclear although some authors have considered that it has a close relationship with the Nembrothinae.

Gymnodorids are similar externally to nembrothids but they lack oral lappets on each side of the mouth and have much reduced gills. They also have non-retractile rhinophores, lack jaw plates and differ considerably in radular morphology. There is no rachidian tooth and often a wide gap separates the innermost lateral teeth on each side (Fig. 16.78B; Kay & Young 1969; Johnson & Boucher 1983). Usually there are one or two inner lateral teeth, and up to 30 ‘outer’ lateral teeth quite different in shape or size to the inner ones. In many species, the innermost lateral on each side is large and hook-shaped and the rest of the teeth are smaller. In others, the inner lateral tooth is small, hook-shaped and sometimes multicuspidate, whereas all the rest are larger and often have a long, recurved rod-like cusp (Fig. 16.78C).

The presence of a gonad separated distinctly from the digestive gland has been used to distinguish *Gymnodoris* from other anadoridoids. All species of *Gymnodoris* for which information is available prey actively on other nudibranchs and related opisthobranchs, such as the sacoglossans. Each species apparently feeds specifically on one prey species.

Family Aegiretidae

These elongate, high bodied nudibranchs have a heavily spiculate, thick body wall (Fig. 16.79A, B). They range in size considerably. Species of *Aegires* seldom are more than 15 mm long whereas *Notodoris* can grow to 140 mm.

This family consists of two genera, *Aegires* and *Notodoris*. The earliest use of Aegiretidae (Fischer, 1883) pre-dates Eliot’s use of Notodorididae in 1910, although both names are still in use. Both genera have a tough spiculate body wall, similar shape and loss of mantle skirt, and smooth rhinophores (Thompson & Brown 1984). It is possible that the similarities reflect a common specialisation for feeding on calcareous sponges rather than a recently shared ancestry.

In *Aegires* (Fig. 16.79B) the mantle skirt is reduced to a slight ridge anteriorly and a row of prominent tubercles around the edge of the body (Bertsch 1980a). Tubercles of the same form occur over the dorsum and sides of the body. The smooth rhinophores can retract into raised tuberculate sheaths. The few gills are protected by a group of modified tubercles and may be simple or tripinnate. The buccal bulb has a thin chitinous lining and there is a single thick jaw plate in the dorsal mid-line. The radula has 10 to 20 lateral teeth on each side of the mid-line. There is no central tooth and the laterals are smooth, non-denticulate and hook-shaped (Fig. 16.79D).

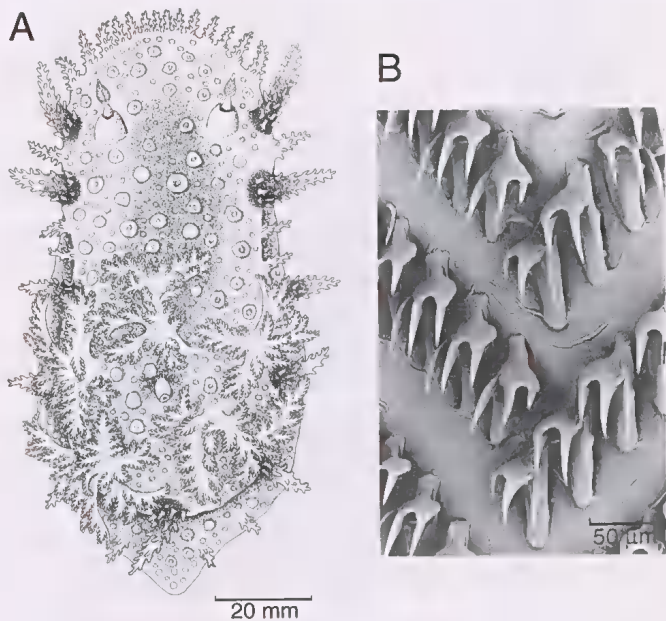


Figure 16.77 Family Polyceridae, subfamily Kalinginae. *Kalinga ornata*: A, animal, dorsal view; B, section of central region of the radula, showing the tricuspidate teeth. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

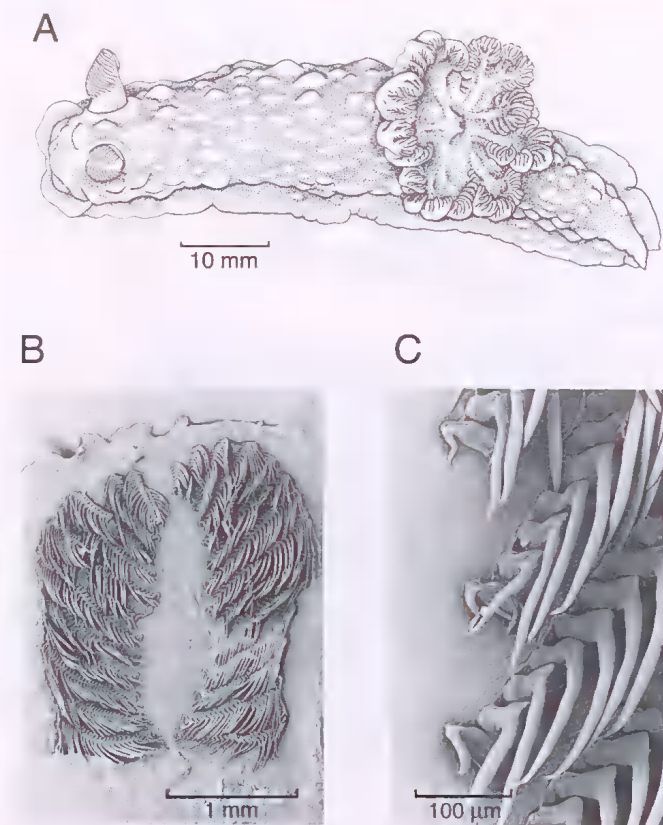


Figure 16.78 Family Gymnodorididae. A, *Gymnodoris plebeia*, dorso-lateral view. B, whole radula and C, inner right teeth of *Gymnodoris okinawae*. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, C, G. Avern]

In *Notodoris* (Fig. 16.79A) there is no sign of the mantle skirt. The dorsum and sides of the body are roughened with some irregular tuberculations (Thompson 1975). The smooth rhinophores are retractile into pockets which can be covered by pallial flaps. The bipinnate or tripinnate gills are protected by the development of a tuberculate, overhanging transverse ridge just anterior to them. The buccal bulb has a thin chitinous lining but jaw plates are not developed. The radula has rows of up to 40 lateral teeth on each side of the tooth-free mid-line. The teeth are simple, non-denticulate and hook-shaped (Fig. 16.79D); in some species, some or all teeth are bifid at the tips.

Notodoris species are found only in the tropical Indo-West Pacific, whereas the genus *Aegires* occurs in tropical, temperate, and polar waters. *Notodoris gardineri* is usually found on or near the calcareous sponge *Pericharax heteroraphis*, on which it feeds. *Notodoris citrina* also feeds on a species of calcareous sponge. Species of *Aegires* also appear to feed exclusively on calcareous sponges (Bertsch 1980a), based on records for *A. punctilucens* (Leucosolenidae), *A. albopunctata* (*Leucilla nuttingi*), *A. albus* (calcareous spicules in stomach), and *A. citrina* and *A. sublaevis* (species of *Clathrina*).

Family Vayssieryidae

This is a small family of small limaciform nudibranchs, less than 5 mm long, in which the mantle skirt is entirely absent and the rhinophores are smooth, contractile and lack sheaths (Fig. 16.80A). Gills are absent and the anus opens dorsally just to the right of the mid-line about halfway down the body. Oral tentacles are absent but there are modified sensory patches on each side of the mouth. Jaw plates are absent and the radula comprises rows of three modified teeth on each side of a small, reduced rachidian plate (Fig. 16.80B). The broad innermost tooth bears four cusps and the second tooth is large and hook-shaped. The outermost tooth on each side is a wide, flattened, acuspidate plate.

The digestive gland is divided into three to four lobes, the heart is not enclosed in a pericardium and the kidney is simplified. The gonad contains usually two lobiform testes and off each of these are two to three slightly smaller spherical ovaries.

Several species have been described in the family, the first from the South China Sea (*Vayssierya felis* Collingwood 1881), and others from New Caledonia (*Vayssierya caledonica*), New Zealand (*Pellibranchus cinnabareus*), Japan, Marshall Island and Hawaii (*Okadaia elegans*) and Australia; some may be synonyms. An undescribed species has been collected (R.C. Willan personal communication). Extensive accounts anatomy have been published by Risbec (1928), Baba (1930, 1931, 1937a) and Ralph (1944) under the latter three names. The identity of the three species has been obscured by differing interpretations of the radular morphology by each author. All three authors have noted that this species has direct development, in which small benthic slugs hatch from the large eggs which are laid in clusters of between two and 25. Baba and Ralph both reported the association of this species with calcareous, tube-dwelling spirorbid polychaete worms, and Young (1969) described how specimens drill through the tube of species of *Spirorbis* and the serpulid worm *Salmacina dysteri* during feeding. Drilling is apparently accomplished by a combination of glandular secretion and rasping by the radula. Although Risbec did not associate *Vayssierya* with spirorbids, it has been found with them in Australia and New Caledonia (W.B. Rudman personal observation).

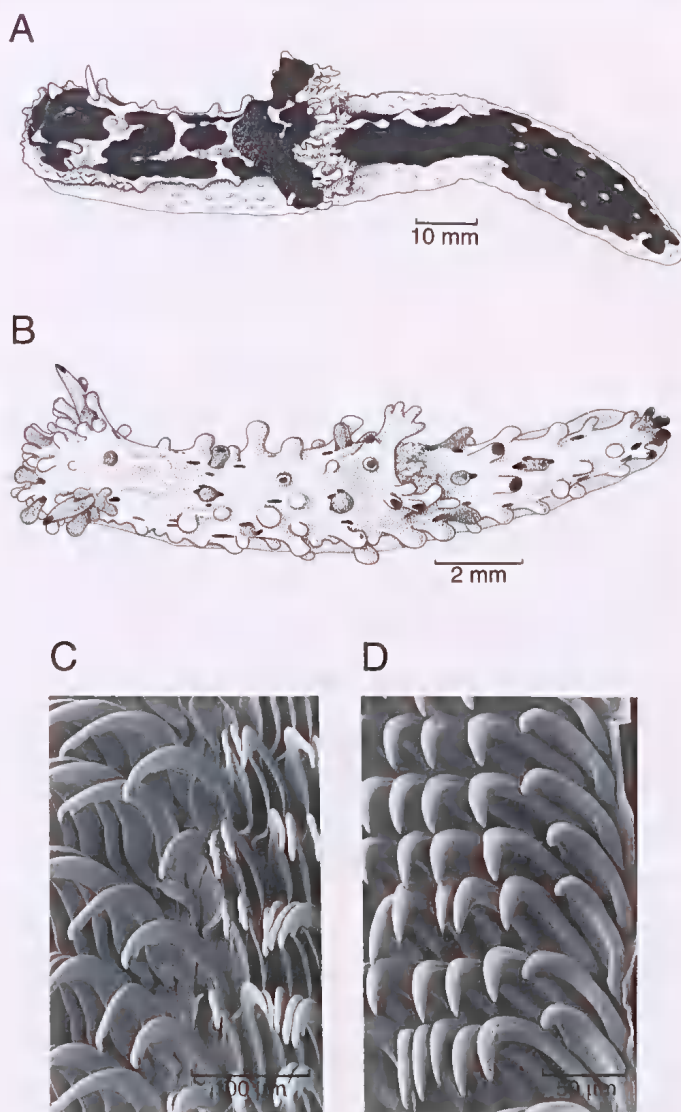


Figure 16.79 Family Aegiretidae. A, *Notodoris gardineri*, dorsal view. B, *Aegires villosus*, dorsal view. C, D, radula sections: C, *Notodoris gardineri*, central region; D, *Aegires citrina*, outer teeth. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C, D, G. Avern]

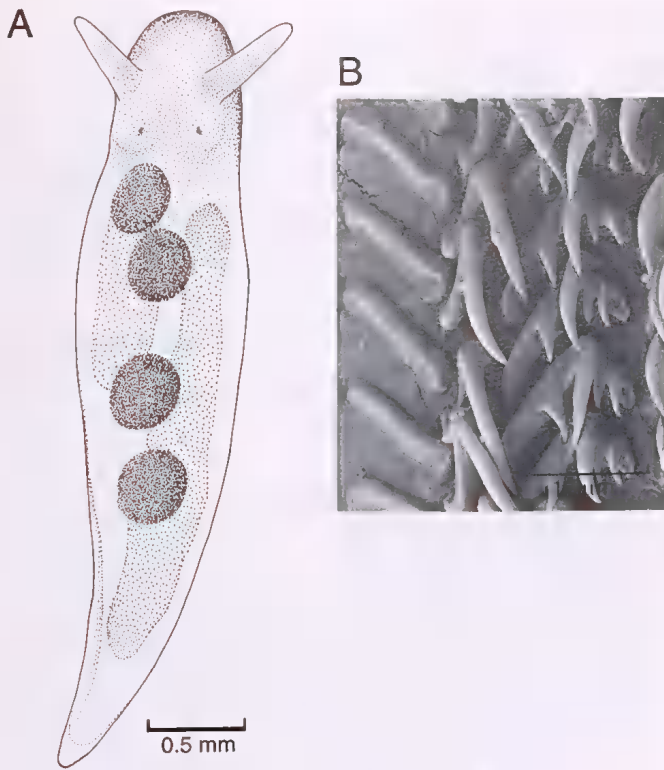


Figure 16.80 Family Vayssiariidae. *Vayssiaria caledonica*: A, animal, dorsal view; B, section of left side of radular ribbon, showing the three different teeth in each half row – the small central tooth is obscured by overhanging teeth from the right side. (A, after photograph by W.B. Rudman)

[A, S. Weidland; B, G. Averil]

Family Hexabanchidae

The family comprises the single genus *Hexabanchus*, with very few, perhaps only one, species. Adults reach over 250 mm in length and have a very broad sinuous mantle skirt (Fig. 16.81A). The lamellate rhinophores retract into separate rhinophoral pockets. The tripinnate gills each insert separately into the dorsum and, although contractile, they lack a pocket into which they can retract. They form a circle around the anal papilla in the dorsal mid-line at the posterior end of the body (Fig. 16.81A, B). The body is soft, and the body wall lacks spicules. The oral tentacles are large rounded plates, papillate along the outer edge.

First described from the Red Sea (Rüppell & Leuckart 1828), reports of species of this genus are common from the whole of the tropical Indo-West Pacific. A species has also been reported from the Virgin Islands in the tropical Atlantic. At least 20 names have been given to Indo-West Pacific forms, but since 1904 there have been suggestions that there are probably less than three and possibly only one species in the genus, based on differences in colour pattern.

The buccal bulb is lined with a thin layer of chitin. A jaw plate, consisting of small chitinous rodlets, is present on each side of the mouth. The large radular ribbon bears approximately 90, simple hook-shaped teeth on each side of the naked mid-line (Fig. 16.81C).

The common Indo-West Pacific species, *Hexabanchus sanguineus*, is well known for its bright red and white mantle skirt which is clearly visible when the animal is swimming; the common name 'Spanish Dancer' refers to the resemblance to the

Superfamily EUDORIDOIDEA

This superfamily is also known as the 'Cryptobranchia', in reference to the presence of a pocket into which the gills can retract completely when disturbed. The morphology of this group is far more uniform than that of the Anadoridoidea. Most species have a wide mantle skirt which hides most of the foot and the small anterior head; the mantle is usually ovate. The animals, all sponge feeders, are relatively slow moving (Edmunds 1971; Thompson 1975). Many have a thick, spiculate dorsal skin. Those that lack this protection have bright colouration combined with defensive mantle glands which apparently provide adequate protection from predation (Rudman 1984a). Members of the Phyllidiidae have lost the dorsal gill circlet, which has been replaced by a set of ventral gills down each side of the body in the lateral groove between the mantle and the foot. In the Phyllidiidae and Dendrodorididae, the radula has been lost and methods of suctorial feeding have evolved. Families placed in this superfamily include the Hexabanchidae, Dorididae, Chromodorididae, Dendrodorididae and Phyllidiidae (Odhner 1968; Thompson & Brown 1984).

The higher taxonomy of the eudoridoid or cryptobranch dorids is not clearly understood. In most review works, at least 15 or 16 families have been accepted but most contain one or very few genera (Odhner 1968; Thompson & Brown 1984), and often the genera seem to bear no close relationship to each other. The system usually adopted is based on Bergh (1892), with little change except for some minor modifications made since that time by later workers, often without justification (Rudman 1984a). There is little point in accepting the many family names until the comparative anatomy of these dorids is more clearly understood.

The following family names, arranged alphabetically, are probably unnecessary: Actinocyclusidae, Aldisidae, Archidorididae, Asteronotidae, Baptdorididae, Discodorididae, Geitodorididae, Halgerdidae, Homiodorididae, Kentrodorididae, Miamiridae, Platydorididae, and Rostangidae.

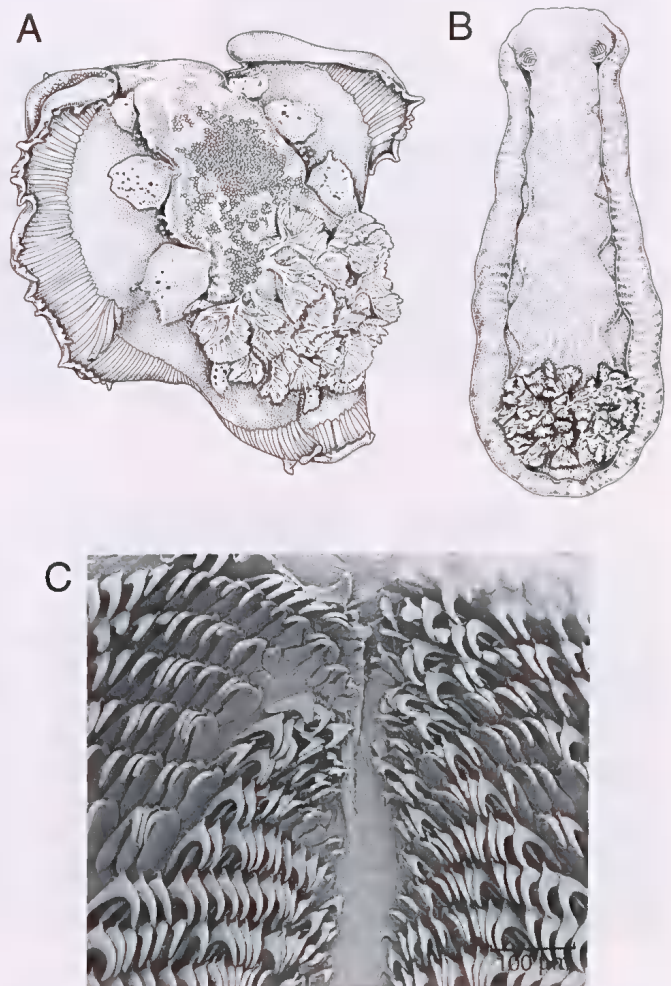


Figure 16.81 Family Hexabanchidae. *Hexabanchus sanguineus*: A, swimming; B, crawling with folded mantle; C, section of radular ribbon, showing serial replication of very similarly shaped teeth. (A, B, after Thompson 1972a)

[A, B, R. Plant; C, G. Averil]

brilliant dress of a traditional Spanish flamenco dancer. Swimming is achieved by a combination of dorso-ventral flexion of the whole body and a rhythmic wave of the mantle skirt down each side (Edmunds 1968b; Thompson 1972a). The bright red and white colours of the mantle skirt are usually hidden when the animal is crawling, for the mantle skirt is folded over such that only the dull mottled colouring of the central dorsum and underside of the mantle show. When disturbed, the mantle is quickly unfolded to display a bright red and white banding pattern. This is generally considered to be a defensive startle response.

Hexabranhus species appear to be generalist sponge feeders (Francis 1980) and graze on a wide variety of inconspicuous encrusting sponges. The range of non-sponge material ingested may explain the many different food items noted in the literature – including Aboul-Ela's (1959) suggestion that members of the genus are exclusively algal feeders.

Family Dorididae

Dorids are small to large, usually ovate and depressed nudibranchs with a broad mantle skirt (Fig. 16.82A, B; Pl. 35.2). The rhinophores are lamellate and retract into separate pockets, often surrounded by a raised sheath, the rhinophoral pocket is either smooth or pustulose, or papillate around the margins. The gills are usually tripinnate and retractable into a common pocket which can be surrounded by a raised sheath. The gill pocket is in the dorsal mid-line near the posterior end of the mantle and also houses the anal papillae.

The mantle is usually relatively thick and is strengthened with a network of fibres and spicules. It can be smooth but is often pustulose, tuberculate or ridged. The mantle surface can have small papillae, microscopic nodules or in some cases is covered in raised tubercles surrounded by a ring of spicules, termed caryophyllidia. Often there are small, scattered secretory glands which are considered to function in defence.

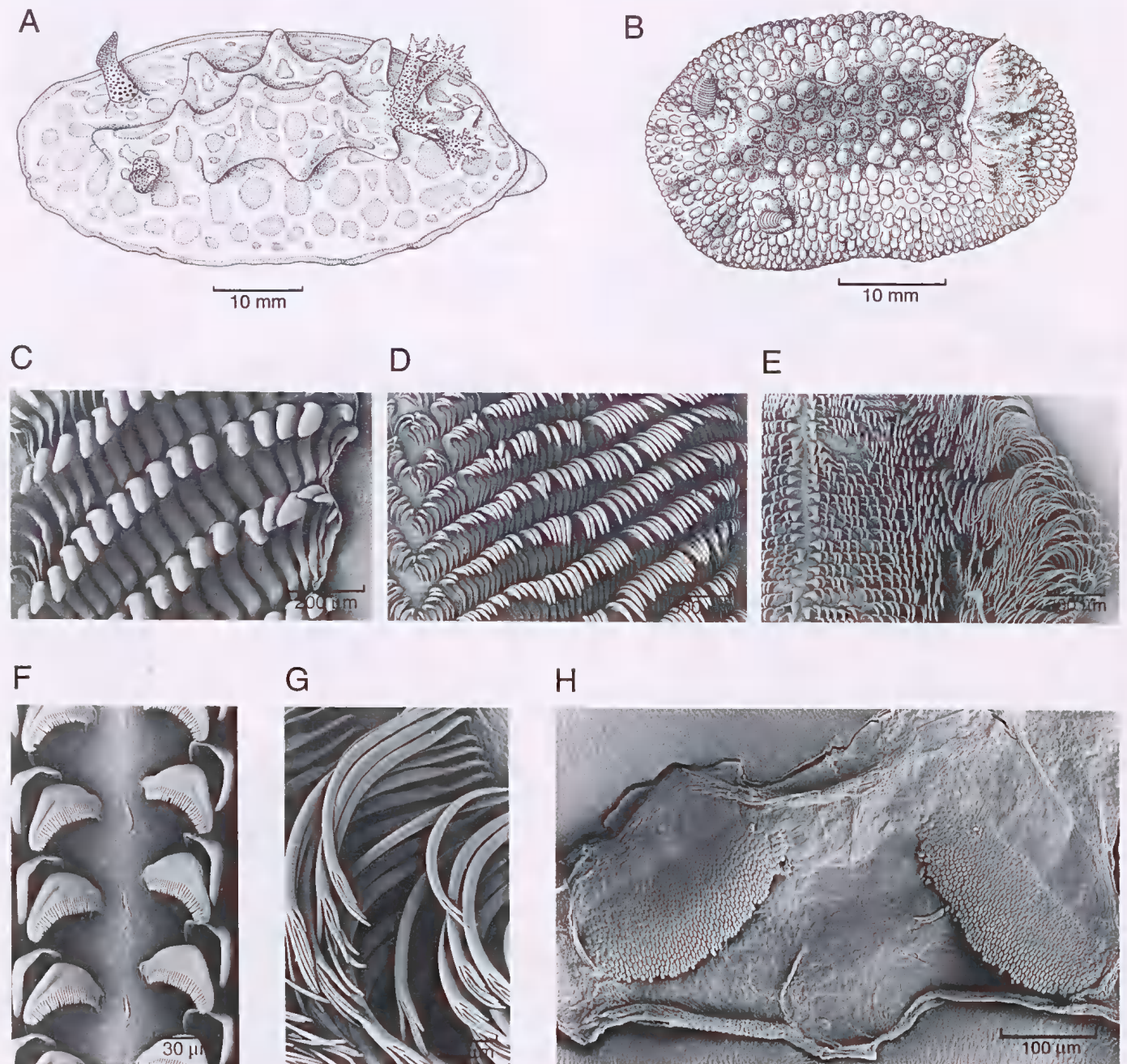


Figure 16.82 Family Dorididae. A, *Halgerda aurantiomaculata*, dorsal view. B, *Hoplodoris nodulosa*, dorsal view. C–G, variation in radular tooth morphology in the Dorididae: C, D, the normal non-denticulate dorid tooth of (C) *Jorunna funebris* – teeth from the right half of the radular ribbon and (D) *Trippa intacta* – section of central region and right side; E–G, *Rostanga calumus*, illustrates the extreme specialisation of some genera, with (E), the central region and right side of radula showing change of tooth shape typical of the genus, the innermost lateral teeth (F), particularly characteristic, and the outer lateral teeth (G), brush-like. H, *Rostanga calumus*, jaw plates consisting of individual chitinous rods. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C–H, G. Averm]

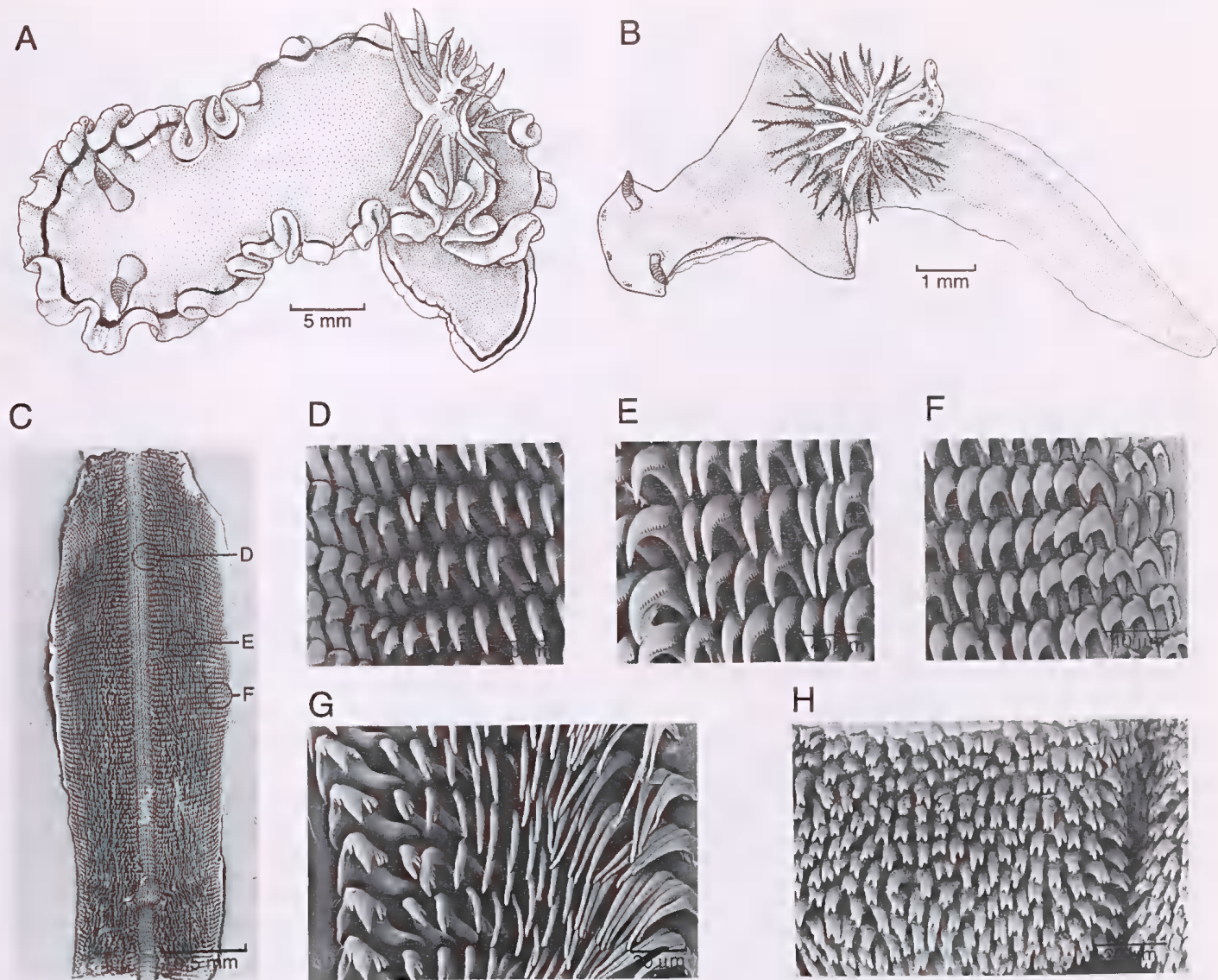


Figure 16.83 Family Chromodorididae. A, *Glossodoris rubroannulata*, dorsal view. B, *Ceratosoma trilobata*, dorsal view. C–G, radula and radular sections showing two major tooth types: C, *Glossodoris rufomarginata*, whole radula; D–F, sections of the right side from the centre (D), midregion (E) and outermost part (F); G, *Noumea romeri*, section of right half of radula. H, *Noumea romeri*, jaw rodlets which are characteristic of the family. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C–H, G. Avern]

The head is usually small and bears a pair of oral tentacles which range in shape from small and conical to large and flattened. The foot is large and often has a lateral split along the anterior edge which divides it into an upper and lower ‘lip’. In many genera the upper ‘lip’ is split into left and right halves. The buccal bulb is usually lined with a thin layer of chitin and there is either a pair of jaw plates (lateral chitinous thickenings on each side of the mouth; Fig. 16.82H) or a continuous ring of thickened cuticle around the mouth. The radular ribbon is usually broad with many rows of simple hamate, or hook-shaped, teeth (Fig. 16.82C, D). In some genera, such as *Rostanga*, the radula is far more specialised (Fig. 16.82E–G). Details of the anatomy of the reproductive system have been used in the classification of genera and ‘families’. However, as with other characters, no clear framework has yet been devised to separate existing genera into reasonable phylogenetic groupings. Many species from a wide variety of genera are known from Australia.

All species for which information is available feed on sponges and, in most cases, each species of dorid has a distinct preference for one or very few species of sponge (Rudman & Avern 1989).

Family Chromodorididae

These nudibranchs range in size from less than 5 mm long (*Pectenodoris trilineata*), to over 120 mm long (*Ceratosoma trilobata*; Fig. 16.83B). The body is usually ovate with a broad

mantle skirt. They are usually brilliantly coloured (Pls 1, 35.4, 35.5, 37.3), and the body wall is thin, usually without tubercles or papillae, non-tuberculate or papillate and without spicules (Fig. 16.83A, B). Defensive mantle glands are well developed and these are arranged in a characteristic way in each genus (Rudman 1984a; see Fig. 16.20A). Rhinophores and gills are retractile into pockets, the rhinophores having a lamellate club. The gills are usually unbranched and show various degrees of elaboration. These may be a simple planar structure with lamellae on the two sides, through gills which are triangular in cross-section with one smooth side, to gills which are quadrangular in section with smooth outer and inner faces.

This large family is well represented in Australian waters with over 100 known species and probably as many presently unnamed. The higher taxonomy has recently been reviewed (Rudman 1984a), and the 20 or so genera are characterised by differences in general shape, arrangement of mantle glands and morphology of gills, foregut, radula, jaw plates and reproductive system. Species are usually characterised by colour patterns, radular morphology and food specificity.

Although most species are ovate with a broad mantle skirt and a thin body wall, some genera show trends towards the gradual loss of the mantle skirt and massive thickening of the body wall. Some species of the genus *Glossodoris* are typically chromodoridid in shape with the mantle skirt elaborated into broad, sinuous folds

16. OPISTHOBRANCHIA

(*G. rufomarginata*) whereas in others the mantle skirt is very reduced and the body wall greatly thickened (*G. atromarginata*) (Rudman 1986b). General trends in mantle skirt reduction and body wall thickening can be seen in a series from *Chromodoris* through *Hypselodoris* and *Risbecia* to *Ceratosoma* where the mantle skirt is reduced to a few lobes including a large medio-dorsal posterior 'horn' (Fig. 16.83B) which is tipped with a large multiple mantle gland. Some genera have dorsal tubercles (*Cadlinella*, *Mexichromis* – Pl. 35.5) and one has lateral papillae also tipped with glands (*Verconia*).

The foregut varies considerably within the family. It ranges in form from the most primitive type, a simple, muscular buccal bulb with a short oral tube as seen in *Chromodoris* and *Cadlina* species, to a situation in which the oral tube is six times the length of the much reduced buccal bulb and radula, as in *Thorunna* and *Ardeadoris* species. The chromodorid radular teeth differ from those of the Dorididae in being strongly denticulate (Fig. 16.83E); there is also much variation between genera in the shape of these radular teeth (Fig. 16.83C–G) and of the jaw rodlets (Fig. 16.83H). Some genera have a reduced rachidian tooth. Jaw plates are present in most and consist of tightly packed clusters of chitinous rodlets, sometimes with bifid or multifid cusps (Fig. 16.83H).

The reproductive system of chromodorids has often been distinguished from that of other eudoridoid dorids by the arrangement of the two sperm sacs (exogenous sperm sac and bursa copulatrix) but the variation now known to exist within the Chromodoridae, and which is used to characterise genera, makes such a simplistic approach unsustainable.

Recent studies by Rudman (1982b, 1983a, 1983b, 1984a, 1985, 1986a, 1986b, 1986c, 1986d, 1987b, 1988, 1990a, 1991a) have shown that in most regions in which they are found, chromodorids occur as groups of similarly coloured species. Such colour-groups often include a number of different genera. In south-eastern Australia for instance there are about 20 species from nine genera which are white with red spots, a colour pattern very uncommon in other parts of the family range (Rudman & Avern 1988; Rudman 1991a). This apparent mimicry is associated with the defensive mantle glands so well developed within the family. Most chromodorid species feed on non-spiculate sponges which produce toxic anti-feedant chemicals for their own defence against predators. The chromodorids are able to ingest these chemicals and accumulate them in their mantle glands where they become effective anti-feedant armour for the nudibranchs.

Chromodorids show a wide range of reproductive strategies from having relatively long-term, planktotrophic veliger larvae to being short-term direct developers. Direct developing species usually have a reduced geographic range. This is evident in south-eastern Australia where many of the endemic species have direct development.

Family Dendrodorididae

These soft-bodied dorids are usually elongate-ovate with a broad mantle skirt (Fig. 16.84). The mantle is usually smooth but can be slightly or very pustulose or tuberculate. The rhinophores have a well-developed lamellate club and each rhinophore has a pocket into which it can retract. The gills are tripinnate or quadripinnate and form an arc around the anus in the postero-dorsal mid-line. The anterior edge of the foot is split transversely, the lower part outlining the sole of the foot as in other cryptobranch dorids. However, the upper 'lip', which is usually split and attached behind and below the head in other dorids, coalesces above and on each side of the small head in dendrodorids, and effectively produces a cavity into which the mouth opens.

The family is characterised by the loss of the radula and the elongation of the buccal bulb into an extensible suctorial pharynx (Edmunds 1971; Thompson 1975). The paired salivary glands at the back of the pharynx are very reduced in size and the bilobed 'ptyaline' gland, a novel glandular organ which lies medially below the pharynx, opens near the mouth.

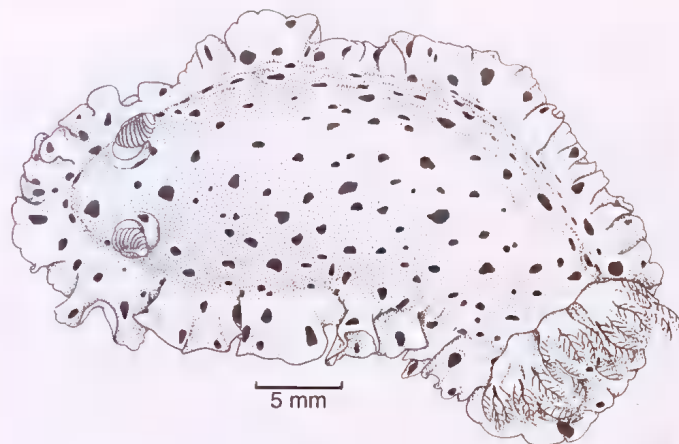


Figure 16.84 Family Dendrodorididae. *Dendrodoris guttata*, dorsal view. (After photograph by W.B. Rudman) [S. Weidland]

Early researchers accepted that there were two genera, *Dendrodoris* and *Doriopsilla*, characterised by the position of the circum-oesophageal nerve ring anterior, or posterior, to the elongate pharynx, but many authors now consider the separation unnecessary. The Dendrodorididae have often been associated phylogenetically with the other suctorial dorid family Phyllidiidae, in the infraorder Porostomata, as discussed under that family. At least 10 species of *Dendrodoris* and three of *Doriopsilla* have been recorded from Australia.

Dendrodorids probably all feed on sponges which are digested externally with secretions from the ptyaline gland. The digested sponge tissue is sucked into the stomach using the elongate pharynx. This type of feeding is difficult to observe and there is usually little in the way of stomach contents to search for sponge spicules or other evidence of previous meals. Morton & Miller (1968) reported that *Dendrodoris citrina* drills into the test of the ascidian *Microcosmus kura* in New Zealand, although the normal diet is considered to be sponges (M.C. Miller personal communication).

Family Phyllidiidae

These are elongate-ovate dorids with a hard, leathery, spiculate and pustulose mantle (Fig. 16.85; Pl. 35.3). Glands in the mantle produce a milky acid secretion. The mantle skirt folds down around the body and encloses the reduced head anteriorly and secondary gill cavities laterally. The rhinophores have lamellate clubs and are retractile into pockets on each side of the antero-dorsal mid-line. The anus is in the dorsal mid-line towards the posterior end of the body, except in the genus *Fryeria* in which it opens in the posterior mid-line below the mantle skirt. The typical dorsal dorid gills have been replaced by a series of up

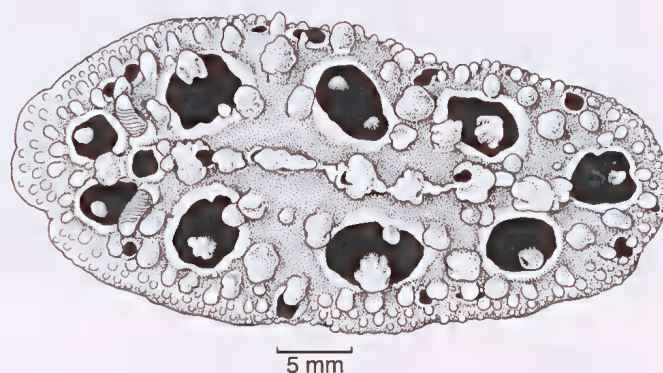


Figure 16.85 Family Phyllidiidae. *Phyllidia ocellata*, dorsal view. (After photograph by W.B. Rudman) [S. Weidland]

to 100 simple gill leaflets along the underside of the mantle in the latero-ventral cavity between the foot and the overlapping mantle skirt. Brunckhorst (1993) reviewed the family, redefining the genera and revising species descriptions.

The foregut is highly modified. The jaw plates and radula have been lost completely. The buccal bulb has become an elongate muscular tube, in which there is a massive development of secretory glands opening towards the posterior end of this tube. The structure of this glandular tissue varies. In some species it is a large mass which encloses the buccal tube and opens through a series of small ducts, in others it is a series of sac-like glands each opening by a separate duct. It may also be incorporated as a very folded glandular lining to the buccal bulb. No distinct paired salivary glands are apparent.

The large glands have variously been named ‘oral’ or ‘ptyaline’ glands but there is no clear understanding of their homology. The relationship of the greatly modified foregut with the buccal bulb and oral tube of less modified dorids is also difficult to interpret. It is possible that the glands are in fact modified salivary glands rather than a novel structure (Wägele 1985).

Phyllidiids occur throughout the Indo-West Pacific and a few are found in the Mediterranean Sea. The family is well represented in Australian waters, especially in the tropics, by species of all known genera, including *Phyllidia*, *Phyllidiella* (Pl. 35.3), *Fryeria*, *Reticulidia* and *Ceratophyllidia*.

Little is known of the ecology and life history of these animals although they are often very common in tropical waters. Most feeding records suggest they are suctorial sponge feeders but it is unknown whether species are specialist feeders on one or a few species of sponge. Phyllidiids are well known for their ability to secrete acrid, acidic and toxic anti-feedant chemicals from their mantle glands. These chemicals are obtained from the sponges they feed on (Gunthorpe & Cameron 1987).

Most workers have followed Bergh (1876) in grouping the families Phyllidiidae and Dendrodorididae, the two families being placed in an infraorder Porostomata or superfamily Dendrodoridoidea. The external similarity of phyllidiids to armininans has led some authors to consider phyllidiids to be very primitive dorids (Thompson 1976; Thompson & Brown 1984). However, the relationship of phyllidiids to other dorids has never been studied adequately and it is equally possible that they are a specialised group that has lost the circumanal gill circle and in which the foregut is modified for suctorial feeding. The relationship with the Dendrodorididae is based solely on the common loss of the radula and the development of suctorial feeding. As the anatomy of the foregut and associated glands is different in each family it is likely that these characters evolved separately in each family. Thus the Porostomata and Dendrodoridoidea are here regarded as artificial groupings.

Suborder DENDRONOTINA

These nudibranchs range from a few millimetres to over 300 mm in length and from large and bulky to small and slender. The most characteristic external feature is the raised sheath, sometimes elaborately developed, around the base of each rhinophore. Usually the head has an oral veil or velum around the anterior end. The mantle skirt is usually absent or reduced to a small ridge bearing a series of paired cerata along each side of the body. The cerata range from simple cylinders to quite elaborate structures which contain branches of the digestive glands and bear gills. In some taxa, such as *Tritonia*, the cerata form dendritic gills. Cnidosacs are usually absent, but have been reported in the Hancockiidae (Odhner 1936, 1973; Thompson 1972b).

The buccal bulb is armed with chitinous jaws. These are either large plate-like structures at the anterior end or more convex acolid-like plates which enclose the buccal bulb. When present, the radula ranges in form from a broad ribbon with many teeth in each row, to a narrow ribbon in which each row is reduced to a

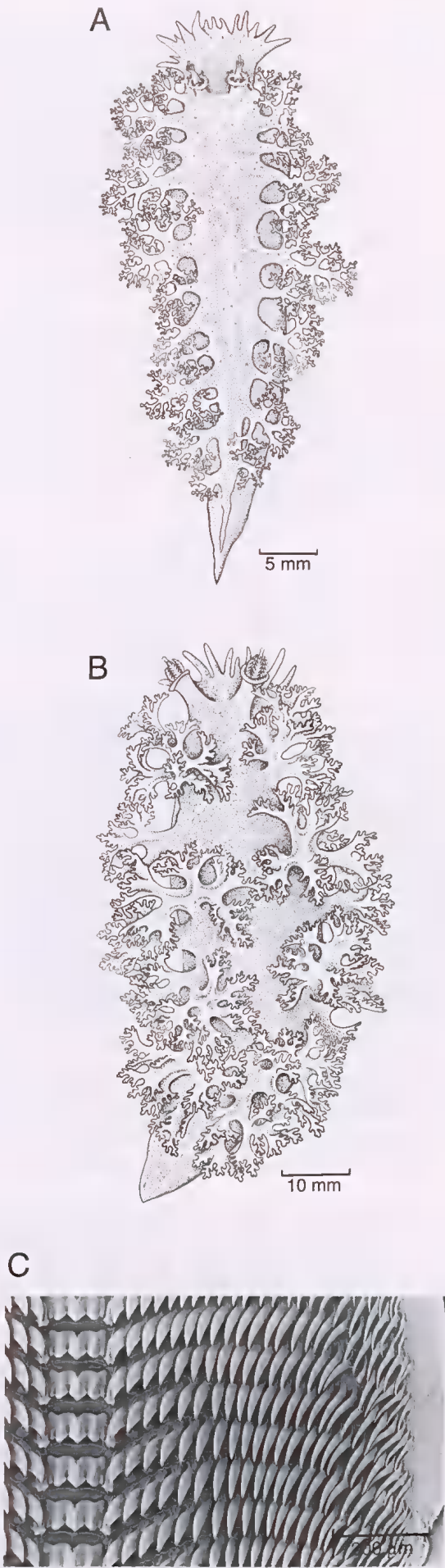


Figure 16.86 Family Tritoniidae. A, *Tritoniopsis elegans*, dorsal view. B, *Marioniopsis* sp., dorsal view. C, *Marioniopsis* sp., section of right side of radula. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C, G. Avern]

16. OPISTHOBRANCHIA

single tooth. Most species feed on cnidarians; some graze on large colonial alcyonarian soft corals and others feed on hydroids. Other cnidarian groups are also represented in the diets of at least some dendronotinans. The family Tethydidae is an exception. Tethydid species have lost the radula; they feed on small crustaceans, which they catch by enveloping them in a large, net-like oral veil. The family Embletoniidae has sometimes been considered as part of the Dendronotina (Miller & Willan 1991), but the presence of nematocysts in the cerata, and the gonad below the digestive gland ducts, have caused most workers to place it in the Aeolidina, a course followed here.

Family Tritoniidae

Tritoniids are soft, usually elongate, dendronotinans in which the edge of the mantle usually bears a series of delicate, branched secondary gills (Fig. 16.86A, B; Pl. 36.8). With few exceptions the mantle skirt is reduced and the body is relatively deep. The well-developed oral veil bears papillae, often branched, along the edge. The oral veil is usually bilobed and at each side the edge of the veil is extended into an enrolled, if short, tentacle (Thompson 1976; Thompson & Brown 1984).

The rhinophoral sheath is usually high with a lobed or scalloped lip. Each rhinophore has a smooth stalk and a characteristic terminal club formed of a ring of vertical papillae, a condition termed 'palmate' by Willan (1988). A stalked knob rises slightly higher than the surrounding papillae from the posterior mid-line of the club. The anal, reproductive and renal openings are on the right side of the body below the mantle edge in the anterior quarter.

In the foregut, a pair of large, heavily chitinised jaw plates enclose the anterior end of the muscular buccal bulb. Large oral glands open at the mouth and a pair of tubular salivary glands open postero-dorsally above the radular ribbon. The radula is usually broad and consists of a median, often tricuspidate, tooth and many pointed lateral teeth (Fig. 16.86C). Often the first lateral tooth on each side is differentiated from the rest and some teeth can be denticulate. Denticulation in some species disappears with age. In some genera there are chitinised plates in the gut variously named 'stomachal' or 'gizzard' plates. They are found in the stomach and form a ring around the entrance to the intestine. The 'holohepatic' digestive gland forms a large discrete mass. It is considered to consist of a right and left lobe, but in most forms these lobes are fused into one.

The generally accepted higher taxonomy of the family is based on Odhner (1936, 1963), but the characters used by Odhner (presence of stomach plates, degree of separation of the digestive gland) are probably inappropriate and a major re-evaluation of the family is required. Species nominally placed in the genera *Marionia* (Pl. 36.8), *Marionopsis* (Fig. 16.86B) and *Tritoniopsis* are known from Australia.

All tritoniids appear to feed on alcyonarian soft corals or gorgonians. Many species are extremely cryptic and mimic the shape and colour of the soft coral on which they feed; the gills often resemble the soft coral polyps closely. Most tritoniids feed only on one species of alcyonarian.

Family Bornellidae

This family contains species with a narrow elongate body in which the mantle skirt is completely absent (Fig. 16.87A). Several pairs of dorsal papillae are present along the dorso-lateral margins of the body. The cerata-like papillae are sometimes branched and usually have one or two gills attached medially near the base. On each side of the mouth the oral tentacle has evolved into a palmate structure with five to 10 pointed papillae in a single or double row. The rhinophoral sheath is high, is usually branched, and is very similar in shape to the paired dorsal papillae along the body. The rhinophoral club is lamellate. The anal, reproductive and renal openings lie ventral to the dorsal papillae in the right anterior quarter of the body.

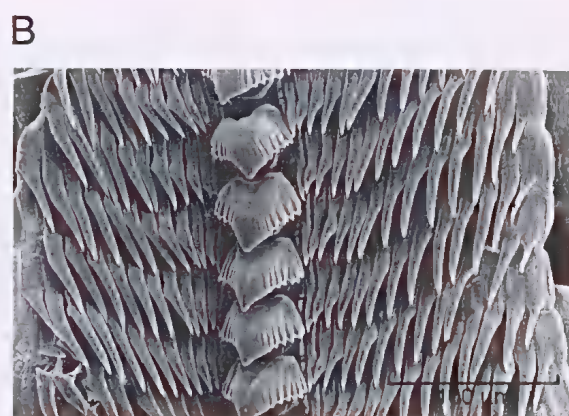
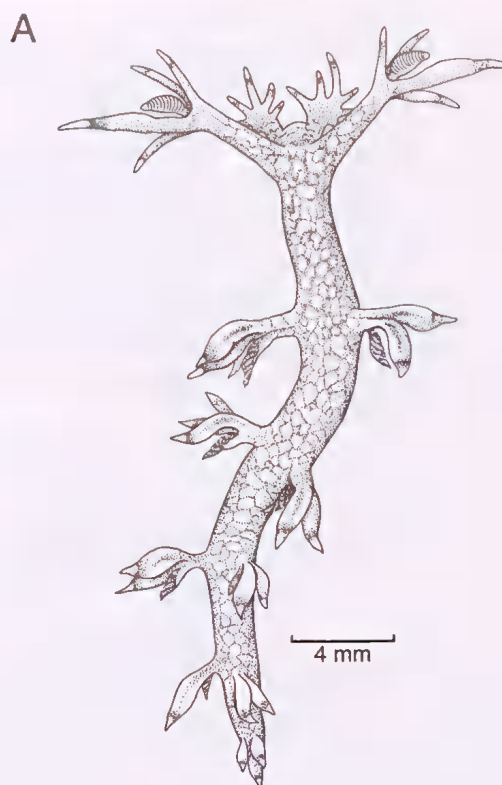


Figure 16.87 Family Bornellidae. A, *Bornella stellifer*, dorsal view. B, *Bornella anguilla*, section of radula. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

The buccal bulb has a thin cuticular lining which is elaborated on each side of the mouth into a pad of rodlets. As well as these dorid-like 'jaws' there are external jaw plates, similar to those of aeolids, which almost enclose the buccal bulb. The radular ribbon is relatively narrow with a prominent median tooth in each row (Fig. 16.87B). The median tooth has one large, heavily denticulate, median cusp. The lateral teeth are narrow and knife-like, sometimes with denticles along the inner edge of the innermost lateral tooth. In the genus *Bornella*, a muscular chamber, lined with chitinous spines, separates the stomach from the intestine. The digestive gland opens into the stomach through three ducts which lead to two small anterior and one large posterior lobe. The digestive gland is essentially a large mass within the body cavity, but small tubular branches lead from it into some or all of the dorsal processes (compound cerata).

Many species of the genus *Bornella* have been described from the Indo-West Pacific (Rudman 1984b), but most are considered to be synonyms of the common *Bornella stellifer* (Fig. 16.87A). Species are also known from both coasts of tropical America (Bertsch 1980b), and a second genus, *Pseudobornella*, is known only from Japan. Little is known of their ecology and behaviour, but some

species are reported to feed on small hydroids. When disturbed some species are able to swim rather non-directionally by lateral flexion of the body. The specific name of *Bornella anguilla* refers to its eel-like swimming through the propagation of a lateral wave down the body (Johnson 1984).

Family Marianinidae

The Indo-West Pacific species, *Marianina rosea*, is the sole member of this family (Fig. 16.88). It grows to about 15 mm in length. It is a narrow, elongate aeolidiform nudibranch, in which the oral veil is replaced by a pair of long, tapering inner tentacles and a pair of shorter, ventrally grooved outer tentacles. Each of four clusters of tapering cerata along each side of the body consists of two cerata. The rhinophoral sheaths are high and bear a tapering antero-lateral projection at the outer edge. The rhinophoral club consists of a ring of vertical papillae with a stalked knob in the posterior mid-line, as in the Tritoniidae. The mantle skirt is reduced to a small pallial ridge running from the rhinophores along each side between the cerata (Carlson & Hoff 1973b; Burn 1974c).

The jaws are arranged at the anterior end of the buccal bulb, as in tritoniids. The narrow radular ribbon (Fig. 16.88B) bears a heavily denticulate, single-cusped median tooth and four or five slender pointed lateral teeth on each side, a form reminiscent of the Bornellidae. The arrangement of outer denticles on the first lateral tooth is very similar to that described for *Pseudobornella*. The two anterior lobes of the digestive gland are fused, but enter the stomach by separate ducts. A branch of this anterior digestive gland extends into the anterior pairs of cerata on each side. The posterior digestive gland lobe is unbranched. Some cuticularisation of the stomach lining is reported by Odhner (1936), but its nature needs further investigation. *Marianina rosea* is reported to feed on hydroids.

Odhner (1936) noted some anatomical similarities between *Marianina* and the Tritoniidae, but felt that aspects of the cerata, digestive gland and radular morphology were sufficiently distinct to warrant separation at the family level. Willan (1988) considered that *Marianina* should be placed in a separate subfamily of the Tritoniidae on the grounds that the degree of separation of the right and left digestive gland lobes is unimportant. However, he did not address the significance of other differences, such as those of the dorsal papillae, the gill-less cerata in *Marianina* and the distinct tritoniid gills, or the difference in radular type. Given the overall lack of understanding of dendrotoninans, the Marianinidae are retained here as a distinct family, with some features shared with tritoniids and some with bornellids.

Family Hancockiidae

Species of the only genus, *Hancockia*, are usually less than 20 mm long, elongate and aeolidiform, and have a long narrow foot (Fig. 16.89A). There is no distinct oral veil, but each side of the mouth bears a rounded palmate pad with five to seven digitate projections. The rhinophoral sheath is high and its edge is fringed with up to ten tapering papillae. The rhinophoral club has a few vertical lamellae and is surmounted by a rounded knob (Marcus, Er. 1957; MacFarland 1966).

The mantle skirt is reduced to an inconspicuous ridge running from the rhinophores dorso-laterally down each side of the body. At regular intervals, large compound cerata arise from this ridge. There are up to seven pairs of compound cerata. Each consists of a cluster of long, tapering, individual cerata arranged in a circle with a common base. The cerata are usually held vertically, but can retract into a tight clump. The anal, renal and genital openings are ventral to the cerata in the right anterior quarter.

The buccal bulb has a thin cuticular lining and, as in the Bornellidae, there is a pad of chitinous rodlets on each side of the mouth. Large external jaw plates are also present. They enclose the buccal bulb partially and have a denticulate cutting edge. The

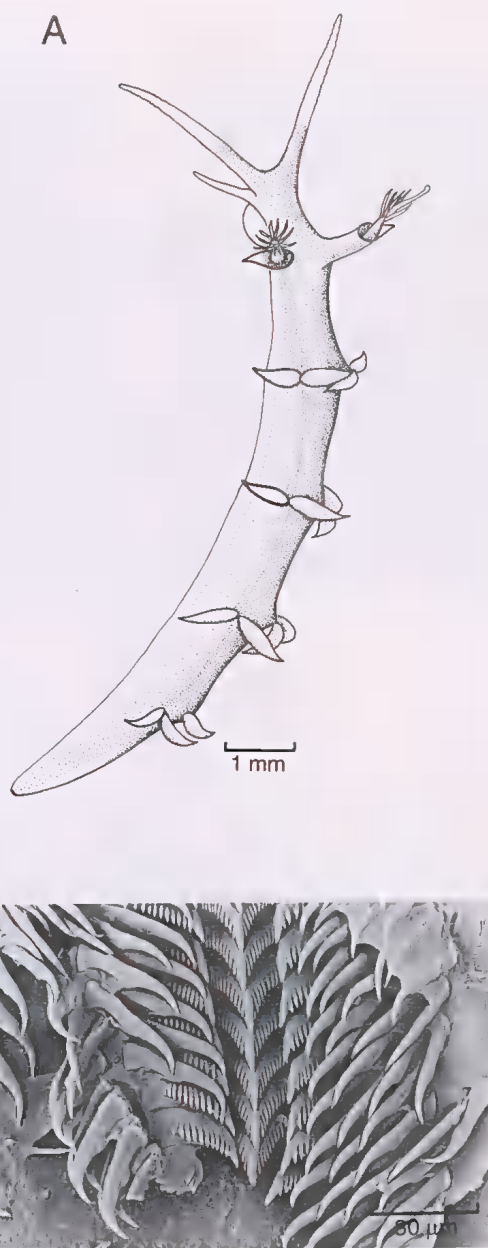


Figure 16.88 Family Marianinidae. *Marianina rosea*: A, animal, dorso-lateral view; B, section of radula. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Averm]

long, narrow radular ribbon has a formula of 1.1.1 (Fig. 16.89B). The rachidian tooth has a large median cusp with five to seven equal-sized denticles on each side. The shape of the lateral tooth on each side varies between the different species, but is basically a smooth irregular triangle with a wide base which rises to a pointed cusp on the inside edge. The anterior end of the buccal bulb is surrounded by oral glands. A large, elongate, ventro-medial oral gland extends posteriorly almost to the posterior end of the body cavity below the viscera. Paired salivary glands open on each side of the oesophageal opening.

The digestive gland is divided into three lobes: the two anterior ones have a common stomach opening; the opening of the large posterior lobe is separate. The anterior lobes lead forward, each giving off branches to the rhinophore and most anterior compound cerata on their respective sides. The posterior digestive gland branches to all the remaining cerata. Within the cerata and rhinophoral sheaths the digestive gland divides into many fine tubules which terminate in small cnidosacs nestled in the epithelium of the body wall. They appear externally as small pustules and contain groups of nematocysts. Thompson (1972b)

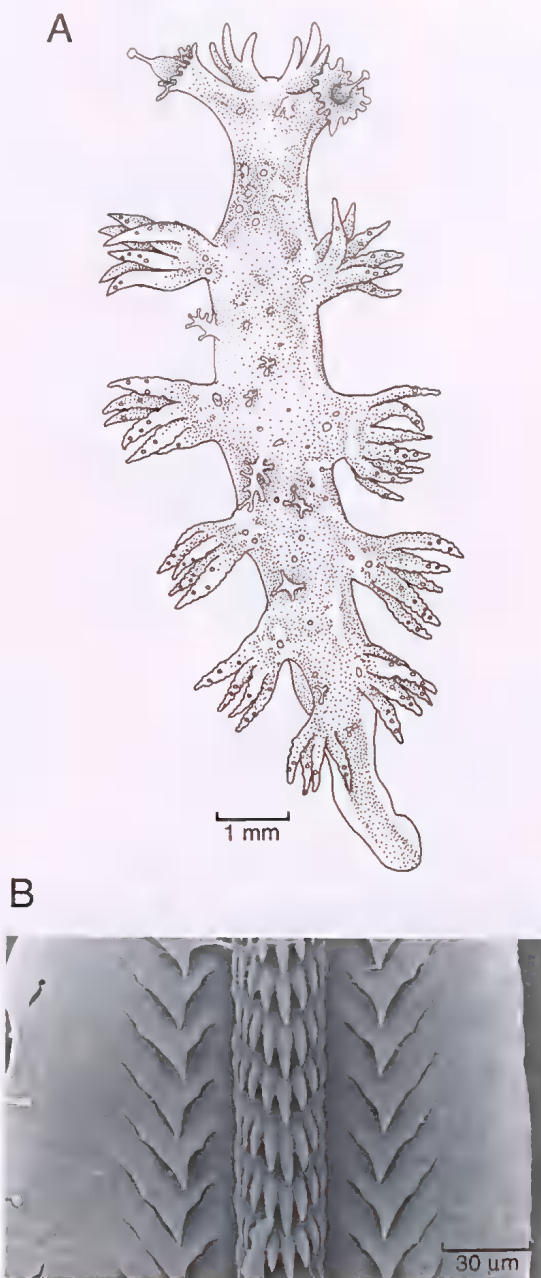


Figure 16.89 Family Hancockiidae. *Hancockia burni*: A, animal, dorsal view; B, section of radula, note close resemblance to the radula of the aeolid genus, *Eubranchus* (see Fig. 16.102). (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

reported that cnidosacs are scattered all over the exposed dorsal surface of the body. There is a swollen muscular chamber at the entrance of the stomach into the intestine. It has a thick chitinous lining which is elaborated into ridges, plates or papillae.

Species of *Hancockia* are known from the temperate and tropical waters of the Atlantic, Pacific and Indian Oceans. They feed on hydroids and store nematocysts from their prey in the cnidosacs in their epithelium. The nematocysts are discharged when the nudibranch is handled roughly. One species is known from Australia.

Family Dotidae

These small aeolidiform nudibranchs are seldom more than 10 mm in length, although a few species reach 30 mm (Pl. 36.6, 36.7). The head is surrounded by an inconspicuous oral veil which is sometimes slightly extended laterally. The rhinophoral sheaths are high with a smooth, flared opening. The rhinophores are simple rods, bluntly rounded at the tip. There is no lateral pallial ridge. Tuberculate cerata are arranged dorso-laterally down each side of the body (Fig. 16.90A). The tubercles are usually arranged

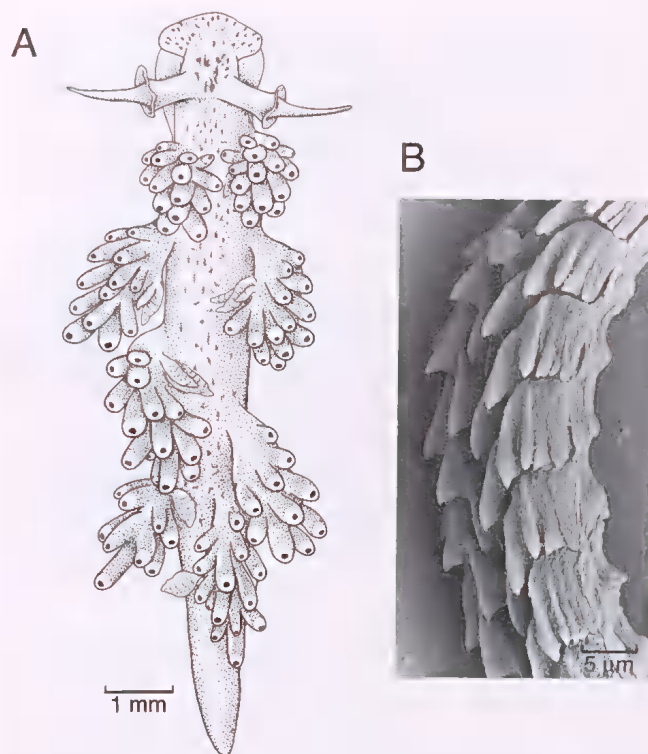


Figure 16.90 Family Dotidae. *Doto ostenta*: A, animal, dorsal view; B, lateral view of a section of the uniseriate radula showing individual teeth locked into a chain. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

in tiers or bands around the cerata. In some species, small simple gills are attached medially to the base of larger cerata. The cerata contain branches of the digestive gland, but there are no cnidosacs. The genital opening is on the right side ventral to the anterior ceras, and the anus and the associated renal opening are found dorso-laterally in the inter-hepatic space. The gonad lies above the median common digestive gland duct (Baba 1971; Thompson 1972b).

The chitinous jaw plates enclose the buccal bulb. The latter contains a long, narrow radular ribbon which consists solely of a row of rachidian teeth (Fig. 16.90B). The teeth have a single, large median cusp usually with a few flanking denticles. The oral gland opens at the mouth and there are paired salivary glands. The digestive gland lies almost entirely within the cerata. From each ceras a short duct leads to the median, non-glandular common duct which opens into the stomach. The digestive gland in the most anterior ceras on each side is considered to be a homologue of the anterior right and left lobes of the ancestral digestive gland. The rest of the digestive gland represents the ancestral posterior lobe (Odhnner 1936). No chitinous armature is associated with the stomach or intestinal opening.

Many species of *Doto* have been described from all oceans of the world. Recent work in Europe suggests that there are probably many more species in the genus than are currently recognised, and that each species occupies a very restricted and specialised niche – probably living on one species of hydroid (Morrow, Thorpe & Picton 1992). Observations by Miller (1980) and Picton (in Thompson & Brown 1984) show that these are suctorial feeders bore holes through the hydroid perisarc to suck out the coenosarc fluid, unlike most hydroid-feeding aeolids which simply bite off the polyps. At least six species are known from Australia.

Family Scyllaeidae

The dorso-lateral mantle ridge is produced into one or two large flattened lobes on each side in scyllaeid nudibranchs (Fig. 16.91A). The inside (dorsal) face of each ceras carries dendritic, tubular, transparent 'gills'. A bilobed oral veil may be present and the rhinophoral sheaths, although smaller, tend to approximate the cerata in shape. The large sheaths are quite flattened, although

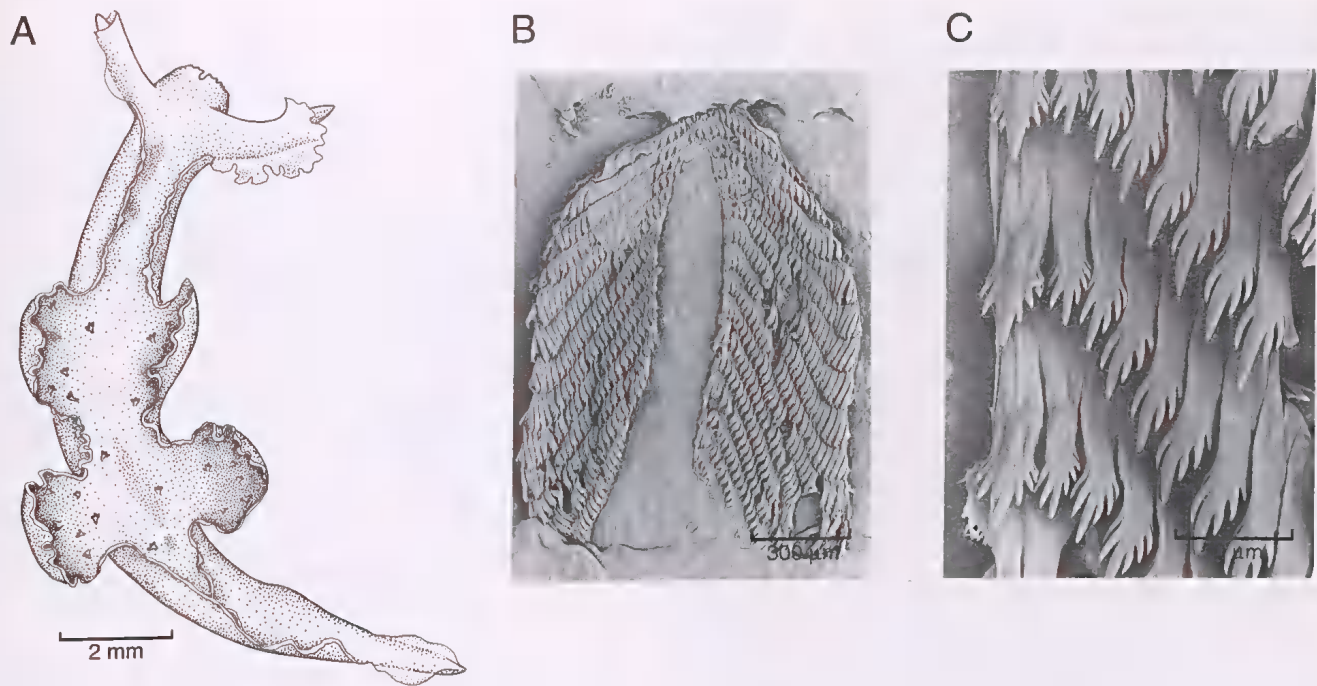


Figure 16.91 Family Scyllaeidae. *Scyllaea pelagica*: A, animal, dorsal view; B, whole radular ribbon; C, inner right teeth of radula. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, C, G. Avern]

tubular, and sometimes have a posterior keel. The rhinophoral club is relatively small and bears a few horizontally arranged lamellae and a terminal stalked knob. A medio-dorsal keel may be present posterior to the cerata (Baba 1937b).

The genital opening is on the right side, antero-ventral to the first ceras. The anus and associated renal duct open midway along the body, ventral to the single right ceras in *Crosslandia*, and between the two right cerata in the other genera (Thompson & Brown 1981).

The buccal bulb is partially enveloped by a pair of chitinous jaw plates. The radular formula is n.0.n (Fig. 16.91B) or n.1.n; there are seldom more than 30 lateral teeth in each half row. When present, the central tooth is an elongate plate bearing a single pointed cusp with four to five denticles on each side. The lateral teeth are more elongate, slightly asymmetrical and increase in size laterally along the row (Fig. 16.91C).

The unbranched digestive gland usually consists of two or three large lobes. There is a band of chitinous plates at the junction of the intestine and the stomach. The three recognised genera, *Scyllaea*, *Notobryon* and *Crosslandia*, occur in Australian waters. All species are considered to feed on epiphytic hydroids growing on brown algae or sea grasses. All species can swim to some extent, and use lateral flexion of the body assisted by the erection and flattening of the rhinophoral sheaths and cerata to increase the dorso-ventral area of the body. The cosmopolitan genus, *Scyllaea*, is usually associated with drifting, oceanic brown algae. Many species have been described in the last 200 years, but recent reviews suggest there are less than five species in the genus. *Notobryon* and *Crosslandia* are benthic genera with wide Indo-West Pacific distributions, and the latter has been reported recently from the eastern Pacific (Poorman & Mulliner 1981).

Family Tethydidae

These are small to large elongate dendronotinans growing to 150 mm in length (Fig. 16.92). The family is also known under the name Fimbriidae and was previously known by the preoccupied name Tethyidae (ICZN 1981). It is characterised by a large oral hood fringed with tentacles which is used to capture small crustacean prey (Pl. 36.5). The rhinophoral sheaths are either cylindrical or flattened to approximate the shape of the cerata. There is sometimes a posterior papilla on the edge of the sheath. The rhinophoral club is relatively small and bears horizontal lamellae (Gosliner 1987b).

There is a row of cerata along each side of the body. These are usually broadly flattened except at the base where they are cylindrical (Fig. 16.92), but in some smaller species the cerata are more inflated and tuberculate as in the Dotoidae. The cerata are fluid filled, usually without branches of the digestive gland. The inside (dorsal) face of the cerata (and sometimes the outside) bears scattered, branched gills in *Melibe*, which are similar to those of the Scyllaeidae. Sometimes they are also present over the whole dorsal surface of the body. In *Tethys*, the gills are more complex; a pair is usually present at the base of each of the larger cerata. The anal, genital and renal openings are in the right anterior quarter of the body ventral to the cerata.



Figure 16.92 Family Tethydidae. *Melibe mirifica*, dorsal view. (After photograph by W.B. Rudman) [S. Weidland]

16. OPISTHOBRANCHIA

The foregut is greatly modified. The mouth opens in the middle of the great oral hood. The radula is absent, but there are chitinous thickenings on each side of the mouth in some species, and apparently true jaw plates occur in others (Gosliner 1987b). The oesophagus is greatly shortened and leads back to a capacious stomach which usually bears a band of chitinous plates around the opening to the intestine. The digestive gland usually forms two or three masses which spread throughout the body cavity, especially in the posterior half where branches of the gland interdigitate with the gonad. In a few species the digestive gland branches into the cerata.

The family contains two genera, *Tethys* and *Melibe*. The latter is represented in Australia by at least three species (Burn 1957b, 1960c). The larger species are able to swim by lateral flexions of the body aided by the erection of the cerata to increase the dorso-ventral surface area. Swimming seems to be an escape response usually effected after a major disturbance. Another response to physical disturbance is the shedding of some or all the cerata. These can regenerate.

Some species are associated with soft-bottom communities, often seagrass beds whereas others are usually found in thickets of brown algae. They feed by capturing small crustaceans in their large extensible oral hood. One of the most fascinating of many studies on the west coast American species *Melibe leonina* concerns metamorphosis and feeding. Within two days of settling from the plankton the oral hood is well developed and is used to capture protozoans as food (Bickell & Kempf 1983). As it grows the young slug feeds on larval crustaceans and later on adults of microcrustaceans such as copepods and amphipods.

Family Phylliroidae

Members of the family are highly modified, pelagic dendronotinans in which the cerata are lost and the foot is absent or very reduced (Fig. 16.93; Pl. 30.1). They are laterally compressed and lanceolate in shape, and small to medium in size, seldom more than 40 mm long (Lalli & Gilmer 1989).

The body wall is transparent, there is no mantle skirt, and the large, smooth, unsheathed rhinophores are continuous with the body wall. A rounded ledge above the mouth immediately anterior to the rhinophores represents the oral veil. In *Cephalopyge*, a conical papilla in the ventral mid-line just below the mouth represents the posterior end of the foot. There is no indication of a reduced foot in *Phylliroe*.

Chitinous jaws cover the anterior part of the muscular buccal bulb. The very small radular ribbon of *Cephalopyge* has a formula of 1.1.1. This structure is larger in *Phylliroe*, with a formula of 6.1.6. The median tooth bears a single cusp with many denticles on each side. The lateral teeth are much more elongate and comprise a long smooth cusp emerging from a triangular base which is denticulate on both sides.



Figure 16.93 Family Phylliroidae. *Phylliroe bucephalum*, lateral view. (After photograph by W.B. Rudman) [S. Weidland]

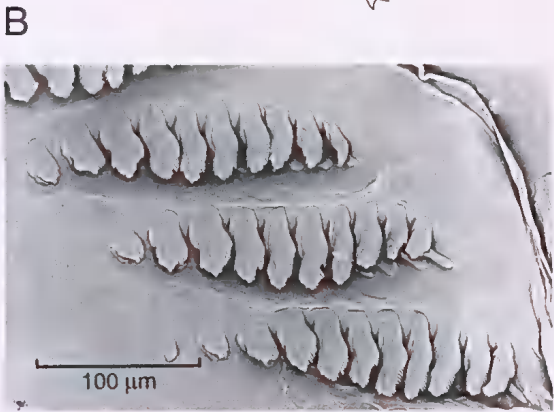


Figure 16.94 Family Lomanotidae. *Lomanotus* sp.: A, animal, dorsal view; B, three rows of teeth on right side of radular ribbon. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

The digestive gland lobes are modified to form long tubular processes. The two 'anterior' lobes have become a pair of dorsal lobes stretching from one end of the body to the other, whereas the 'posterior' lobe has moved ventrally. In *Cephalopyge*, it consists only of a long posterior section, but in *Phylliroe* it has an anterior lobe as well. The anus opens in the dorsal mid-line just posterior to the rhinophores in *Cephalopyge* and at midlength on the right side in *Phylliroe*.

Our knowledge of this cosmopolitan family of pelagic dendronotinans is based on very few specimens, mostly examined after years of preservation (Dakin & Colefax 1936). Steinberg (1956) observed that the six known species of *Cephalopyge* were based on less than 30 specimens from eleven collections. Members of the family are assumed to feed on pelagic hydrozoans, medusoids and siphonophores. The young of *Phylliroe* are reported (Boss 1982) to parasitise the medusae of *Zanclea*. Juveniles are found attached within the bell of the *Zanclea* on which they feed (Martin & Brinckmann 1936) and where they remain until adulthood. Adults are free-living, and feed on *Zanclea*, as well as other medusae and plankton, including the larvacean *Oikopleura*. They are usually found near the surface at night and luminesce brilliantly. Sentz-Braconnot & Carré (1966) indicated that *Cephalopyge* species probably feed exclusively on siphonophores in the genus *Nanomia*.

Family Lomanotidae

The edge of the mantle is developed into a sinuous ridge on each side of these elongate dendronotins, from the rhinophores to the posterior tip of the body (Fig. 16.94A). Along the edge of the ridge are short pointed cerata which lack gills. The head bears one or two pairs of oral tentacles and the rhinophores arise from a tall sheath with papillae around its rim. The rhinophoral club bears fine transverse lamellae and is surmounted by a bluntly rounded knob.

The anus opens just below the mantle ridge on the right side of the body about one-third of the way down the body just posterior to the pericardium. The anterior corners of the foot may be rounded or tentacular.

The elongate jaws almost enclose the buccal bulb and bear rows of multi-denticulate plates along the masticatory border. Numbers of teeth range widely in association with body size, as shown by the radular formula: (24–11).0.(11–24) (Fig. 16.94B). The innermost tooth on each side is short; a long pointed cusp arises from a broad blade which is denticulate on both sides. The other teeth are similar in shape, but have a reduced central cusp. The blade length increases laterally along the row, reaching its maximum about three teeth from the end.

One species, recorded as *Lomanotus vermiformis*, is known from Australian waters (Willan 1988). Originally described from the Red Sea, it apparently has a circumtropical distribution and now is considered a synonym of *L. stauberi*, a species known from both coasts of central America (Gosliner & Bertsch 1985). It is always found on the aglaopheniid hydroid *Lytocarpus philippinus*, to which it clings with its narrow grooved foot. It produces a sticky mucous thread when crawling and thrashes violently with powerful lateral flexions of the body when removed forcibly.

Two European species are reported to feed on hydroids of the genus *Nemertesia*. One of these species, *Lomanotus genei*, apparently grows to 90 mm (Thompson & Brown 1984), much larger than *L. vermiformis* which is not known to exceed 25 mm in length.

Suborder ARMININA

The Arminina is the smallest and most recently introduced major subdivision (Odhner 1934) within the Nudibranchia. It is also the most unsettled. It embraces taxa with long optic nerves and the primitive characteristics of an oral veil and lateral anus. These taxa appear to have been grouped together because they cannot be conveniently 'pigeon-holed' elsewhere. Two very divergent lineages are included: the Euarminoidea and the Metaminoidea. The superfamily Euarminoidea, comprising the Arminidae and Doridomorphidae, is characterised by a large mantle without cerata, gills (when present) beneath the mantle brim, and retractile rhinophores (Lance 1962; Odhner 1968). The superfamily Metarminoidea, comprising the Charcotiidae, Madrellidae, Dironidae, Pinufiidae, Goniaeolididae, Zephyrinidae and Heroidae, has aeolidiform members with a reduced mantle, cerata on the notum, and non-retractile rhinophores (Pruvot-Fol 1954;

Odhner 1968). No synapomorphies unite these two lineages. The Dironidae, Goniaeolididae and Heroidae are all very small families that do not occur in Australia or Australian territories and therefore are not treated further here; information on them is given by Boss (1982). As is the case with most of the Australian nudibranchs, armininans are in need of taxonomic revision.

Family Arminidae

Arminids are elongate nudibranchs, with a distinct oral veil, often with longitudinal ridges on the notum (Figs 16.2I, 16.95), and a cladohepatic digestive gland from which diverticula extend to the sides of the mantle. The mantle is large with thickened, expansive margins and its dorsal surface bears a series of strong, longitudinal ridges that are most often black and white lined.

Synonyms include Pleurophyllidiidae, Pleuroleuridae, Heterodorididae and Atthilidae. (The name *Pleurophyllidia* had long been in use for the principal genus *Armina*). Besides *Armina*, the family probably contains only two other genera – *Dermatobranchus* (Pl. 35.1) and *Heterodoris* (Willan 1981b; Miller & Willan 1986). Revisions encompassing non-Australian members of this family include the works of Bergh (1892), Ev. Marcus & Er. Marcus (1966b), Baba (1976) and Miller & Willan (1986). Within Australia, Basedow & Hedley (1905) described a new species and one can find mention and illustrations of arminids in Burn (1964a, 1989), Gillett & Yaldwyn (1969), Coleman (1975, 1981) and Willan & Coleman (1984).

Some species of *Armina* may attain 100 mm, but half that length is more usual for members of the family. The body is narrowly elongate, and the mantle and foot are approximately equal in length and connected posteriorly. The oral veil has short, lateral tentaculate lobes and there is a fringe of papillae near the base in some species. A transverse flap, lobe or ridge, termed a caruncle, is present in some species immediately anterior to the rhinophores. The rhinophoral clavus, or club, consists of a compact series of primary vertical lamellae, subdivided into secondary and tertiary plates. Longitudinal mantle ridges are present in most species of *Armina* and *Dermatobranchus*, but in both genera they can be replaced by irregular pustules, or the notum can be smooth in *Dermatobranchus*. The margin of the mantle has numerous pallial glands or cnidosacs (the presence of nematocysts is sometimes contested). Anteriorly in *Armina*, the undersurface of the mantle brim bears leaf-like gills, and a complex system of oblique folds (= secondary lamellae) is present medially and posteriorly. *Dermatobranchus* has no gills or ridges beneath the mantle rim.

The pear-shaped pharyngeal bulb contains two, large, thick, wing-like jaws and a broad radula with one central tooth and up to 50 lateral teeth on each side. A large salivary gland is situated on each side of the oesophagus behind the circum-oesophageal nerve ring, but there are no oral glands. The small stomach curves to the left and is confluent with the main posterior duct of the digestive gland. Both right and left lobes of the digestive gland are dendritic, and the terminal diverticula extend outwards to the mantle brim. The ovotestis, which consists of a series of spherical

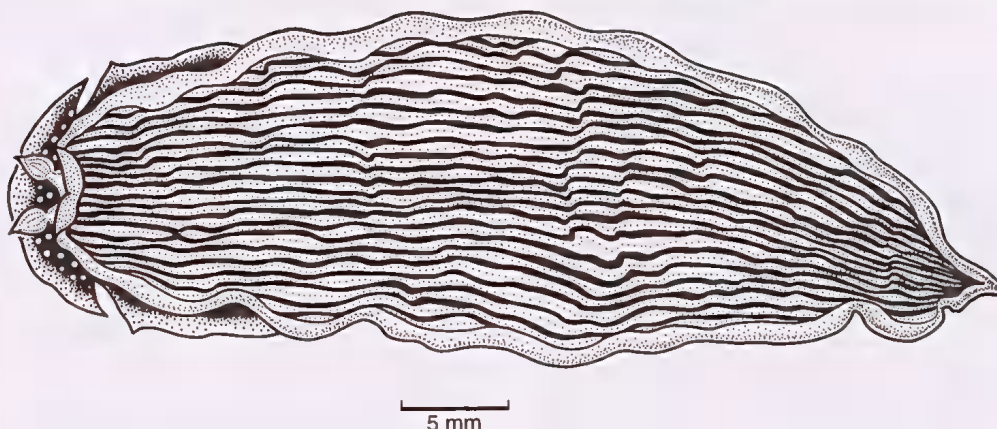


Figure 16.95 Family Arminidae. *Armina* sp., dorsal view. (After photograph by R.C. Willan)

[L. Newman]

16. OPISTHOBRANCHIA

follicles, empties into an hermaphroditic duct. Other organs of the reproductive system are an ampulla, nidamental gland mass, vagina, bursa copulatrix, vas deferens and penis. The vas deferens is prostatic for most of its length and the penis is large and simple.

Specimens of *Armina* are caught regularly by prawn trawlers in northern Australia. Apparently they eat sea pens (Pennatulacea) (Bertsch 1968; Morton 1979), using their strong jaws and radula to rasp the flesh. *Renilla koellikeri*, an eastern Pacific sea pen, produces luminescent flashes when being eaten by *Armina californica*.

The Arminidae are a tropical family with five recorded and about 15 undescribed species from Australia (R.C. Willan personal observation). Probably the commonest species is *Dermatobranchus fortunata* which can be found beneath dead coral slabs at the reef crest on coral islands on the Great Barrier Reef. Only *Armina cygnea* and *Dermatobranchus pulcherrimus* are known from temperate waters; the former is unusual because it is one of the few opisthobranchs known to occur all around Australia but not elsewhere in the western Pacific Ocean.

Family Doridomorphidae

A single tropical species, *Doridomorpha gardineri*, is included in the family Doridomorphidae (Fig. 16.96). It is a small, doridiform nudibranch without oral tentacles, gills or accessory respiratory structures, and is found only on its food species, the coenothecalian coral *Heliopora coerulea*, to which it bears a remarkable resemblance. Synonyms for the family name are Doridoeididae and Doridoididae.

Doridomorpha gardineri was first described from a single preserved specimen from Rotuma Island, north of Fiji (Eliot 1906b). Details of the anatomy were provided by Eliot & Evans (1908), Er. Marcus & Ev. Marcus (1960) and Rudman (1982a). Investigations of the first living specimens, based on material from Guam and Exmouth, dispelled any suggestion that *Doridomorpha* is related to true dorid nudibranchs (Rudman 1982a). Its ramifying digestive gland is indicative of membership of the Cladohepatica as are the lateral anus, wing-like jaws and single exogenous sperm receptacle. The presence of long optic nerves and an arminid-like radula suggest placement in the Arminina. In all probability, the dorid-like body of *Doridomorpha* arose through secondary simplification and flattening.

Adult *Doridomorpha* attain a maximum length of 9 mm. The body is almost circular with a smooth, flat mantle which bears a raised central hump. Anteriorly the mantle continues as an uninterrupted arc anterior to the smooth rhinophores, as in dorids – presumably this condition represents fusion of the mantle and oral veil. The mantle is light brown with numerous, opalescent green spots and it is patterned to match the host coral. The mouth is a simple pore in front of the foot. Eliot & Evans (1908) described the basic morphology of the gut and reproductive system. The ducts of the digestive gland emerge from the stomach and the diverticula ramify extensively throughout the dorsal part of the body cavity. The dorsal regions of the body also contain aggregations of zooxanthellae both within the digestive diverticula and in connective tissue spaces between them. No mechanism has been proposed to explain how the zooxanthellae might leave the diverticula. Nothing is known about reproduction or development.

Doridomorpha has only ever been found on *Heliopora coerulea*, though individuals are very hard to detect because they are flattened and well camouflaged. In addition, specimens crawl away from the light remarkably swiftly when a piece of *Heliopora* is examined. The distribution of *Doridomorpha* probably matches that of *Heliopora*, that is, through the tropical Indo-Pacific Ocean (see Veron 1986). In Australia, *Doridomorpha gardineri* has only been found at Exmouth in Western Australia, but thorough searches on *Heliopora* on the northern Great Barrier Reef will almost certainly reveal specimens.

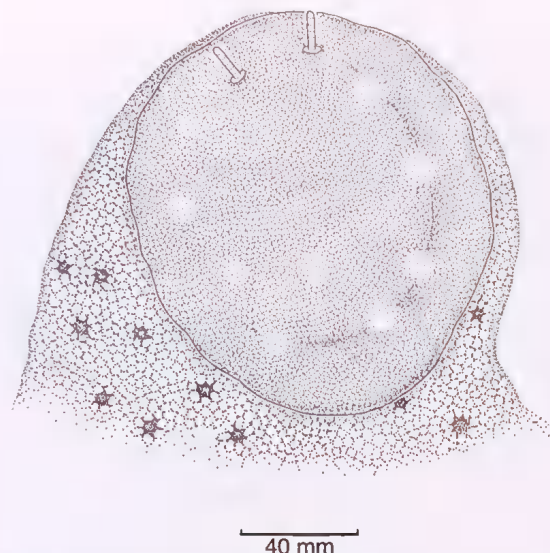


Figure 16.96 Family Doridomorphidae. *Doridomorpha gardineri* on its food, the coenothecalian coral, *Heliopora coerulea*. (After photograph by R.C. Willan) [L. Newman]

Family Charcotiidae

Charcotiid nudibranchs form a small family comprising only three genera. *Charcotia* and *Leminda* are monotypic, and *Pseudotrilonia* includes just two species (Cattaneo-Vietti 1991; Wägele 1991; Wägele, Barnes & Bullough 1995; R.C. Willan personal observation). All have arminiform bodies, simple rhinophores, narrow radulae and cladohepatic digestive glands. Details of anatomy (Fig. 16.97) are given by Vayssière (1906b), Thiele (1912), Odhner (1934), Griffiths (1985), Cattaneo-Vietti (1991), Wägele (1991), Wägele, Barnes & Bullough (1995) and Wägele, Bullough & Barnes (1995).

The body resembles those of arminids or triloniids, in its elongate form with a broad mantle brim which is often thrown into undulations (Fig. 16.97). The mantle and foot are connected posteriorly. The notum is smooth, except in *Charcotia* which has numerous papillae, and the mantle brim has neither dorsal gills nor ventral lamellae. The head bears a large, trapezoidal oral veil which is continuous dorsally with the mantle between the rhinophores. This oral veil is separated from the foot ventrally. The rhinophores are large and simple, and they cannot be retracted below the mantle in either of the two species of *Pseudotrilonia* which have been observed alive (Wägele 1991). In *Pseudotrilonia* and *Charcotia*, a thin strip of glandular tissue is present along the right side from the female genital opening to the tail. The anus is lateral, and opens at midlength or at the posterior third of the body's right flank. The nephridiopore is in line with, and in front of the anus. The separate male and female reproductive apertures are situated antero-laterally, side by side, at the level of the rhinophores. Although the radula is considerably reduced, its formula and tooth shape are characteristic for each genus. *Leminda* has a narrow, smooth rachidian tooth and up to 92 simple lateral teeth on each side; *Pseudotrilonia* has a large denticulate rachidian, a slightly denticulate inner lateral and a smooth outer lateral on each side; *Charcotia* has a denticulate

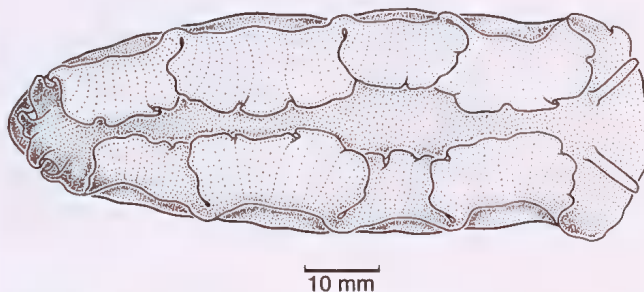


Figure 16.97 Family Charcotiidae. *Pseudotrilonia gracilidens*, dorsal view. (After Wägele 1991) [L. Newman]

rachidian tooth and one denticulate lateral on each side. Generally the jaws are large, thin and wing-like. Four digestive gland ducts emerge from the stomach and branch repeatedly. Their diverticula terminate immediately below the notal surface (well illustrated by Gosliner 1987a) or, in *Charcotia*, within the notal papillae. Details of the reproductive system are given by Vayssi re (1906b), Odhner (1934), Griffiths (1985) and W gele (1991). All species have a single exogenous sperm receptacle, a long, non-prostatic vas deferens, and a large, simple, muscular penis.

Nothing is known of the ecology or life cycle of any member of the family, despite the local abundance of *Charcotia granulosa* and *Pseudotritonia gracilidens* in the immediate subtidal around Signy Island in the Atlantic sector of the Antarctic (W gele, Barnes & Bullough 1995; W gele, Bullough & Barnes 1995), and *Leminda millecra* in 30–40 m at the Cape Peninsula, South Africa (Gosliner 1987a).

Family Madrellidae

The Madrellidae, the sister group to the Zephyrinidae, are a small family of aeolidiform armininans with an oral veil, club-shaped papillate rhinophores and a distinct mantle brim. Cerata encircle the notum and the radula is triseriate. Two species of a single genus, *Madrella*, occur in Australia (*M. ferruginosa* and *M. sanguinea*), two others in Japan (*M. gloriosa* and *M. granularis*), and another in the Mediterranean (*M. aurantiaca*). The monotypic genus, *Eliota* from the Mediterranean, is also in the family. The suggestion by Thompson, Cattaneo & Wong (1990) that *Madrella* is monotypic needs further investigation. *Madrella ferruginosa* (Fig. 16.98) was redescribed by Risbec (1953) and illustrations of Australian specimens of this species were published by Willan & Coleman (1984); illustrations of *M. sanguinea* are available in Gillett & Yaldwyn (1969) and Rudman & Avern (1988).



Figure 16.98 Family Madrellidae. *Madrella ferruginosa*, dorsal view. (After photograph by W.B. Rudman) [R. Plant]

Live specimens of *Madrella* may be up to 18 mm long in Australia. Because of the cerata-covered mantle, they may be mistaken for aeolids, however, the madrellid head carries a large oral veil with a mid-anterior embayment, the mantle is broad, and the cerata are continuous around the anterior margin of the head. The cerata themselves, which are long and independently mobile, often end in a globular cap and they contain branches of the digestive gland. The non-retractile rhinophores are distinctive in that they have a separate stalk and clavus; the latter bears numerous papillae. Such elaboration is analogous to the palmate rhinophores of the Tritoniidae. The foot is broad, its anterior margin is evenly rounded and the top of its posterior extremity usually carries a median longitudinal ridge.

The jaws are large and wing-like. Each row of the radula contains a large cuspidate denticulate rachidian tooth and one denticulate lateral tooth on each side. Branched acinous glands discharge into the rectum. The anus is postero-lateral on the right side. Vayssi re (1902) and Pruvot-Fol (1954) described the reproductive system of the Mediterranean species, in which two exogenous sperm receptacles are apparently present – a bursa copulatrix and a receptaculum seminis. Spawn consists of a loosely wound, gelatinous tangle, not the neat spiral characteristic of other nudibranchs. Nothing is known about development.

When handled, both the Australian species emit a vivid yellow fluid – not red as Willan & Coleman (1984) reported for *M. ferruginosa*. This fluid is produced from glands at the base of the cerata and over the whole body surface; the ceratal glands produce far more than that secreted by the body. Both Australian species are relatively inactive; they can autotomise their cerata when disturbed.

Both the Australian species are essentially intertidal in occurrence. Their geographical distributions overlap in northern New South Wales. *Madrella sanguinea* is a cool temperate species ranging from Cape Naturaliste, Western Australia, to northern Queensland (Burn 1989). It lives under stones in company with its food, the blood-red encrusting bryozoan *Mucopetraliella ellerii*. *Madrella ferruginosa* is a larger, tropical Indo-Pacific species that also lives on encrusting bryozoans.

Family Zephyrinidae

Zephyrinids are highly advanced aeolidiform armininans with distinct oral tentacles and a mid-dorsal anus. Species from two of the four known genera occur in Australia – *Janolus* and *Caldukia* (Burn 1958; Burn & Miller 1969; Willan & Coleman 1984; Miller & Willan 1986). The two remaining genera are *Proctonotus* and *Galeojanolus*. Monographs have been published on zephyrinids from South Africa (Gosliner 1981b) and New Zealand (Miller & Willan 1986). The latter work formally synonymised the family names Proctonotidae, Janolidae and Antiopellidae under Zephyrinidae.

The largest Australian member of the family, an undescribed species of *Janolus*, reaches 50 mm in length. All zephyrinids have elongate, depressed bodies with the notum bearing numerous, slender, sometimes papillose cerata (Fig. 16.99). These cerata occur without interruption around the anterior margin of the head. The broad foot, which is continuous with the notum, extends posteriorly as a tapering tail. Anteriorly, the foot is distinct from the oral veil that overhangs the mouth; the antero-lateral corners of this veil form cylindrical tentacles. The rhinophores are non-retractile and there is usually no clear division into stalk and clavus. Rhinophoral ornamentation separates the genera readily. In *Janolus* the rhinophores are tall, (primitively) lamellate, irregularly rugose or smooth, and an elevated ridge, the caruncle, with presumed sensory function, occurs between the bases of the rhinophores. Those of *Caldukia* are stouter and smooth with a basal expansion that bears bipinnate leaves, and there is no caruncle.

Details of the alimentary system have been provided for *Janolus* by MacFarland (1966) and Miller & Willan (1986), and for *Caldukia* by Burn & Miller (1969); they are very similar. The jaws are large and wing-like, and some species have a few strong denticles on the masticatory border. In *Janolus*, the radula consists of a narrow, usually smooth rachidian tooth and up to 40 smooth laterals on each side. In *Caldukia*, the radula consists of a broad rachidian tooth and six denticulate lateral teeth on each side. The stomach receives three ducts from the digestive gland. Depending on the species and location within the body, the diverticula that ultimately arise from the digestive gland may stop just short of the cerata, enter the ceratal bases, or penetrate deeply into, and branch within, the cerata. Branched glands which are present in most species discharge into the rectum. The anus opens on a papilla in the mid-line posteriorly.

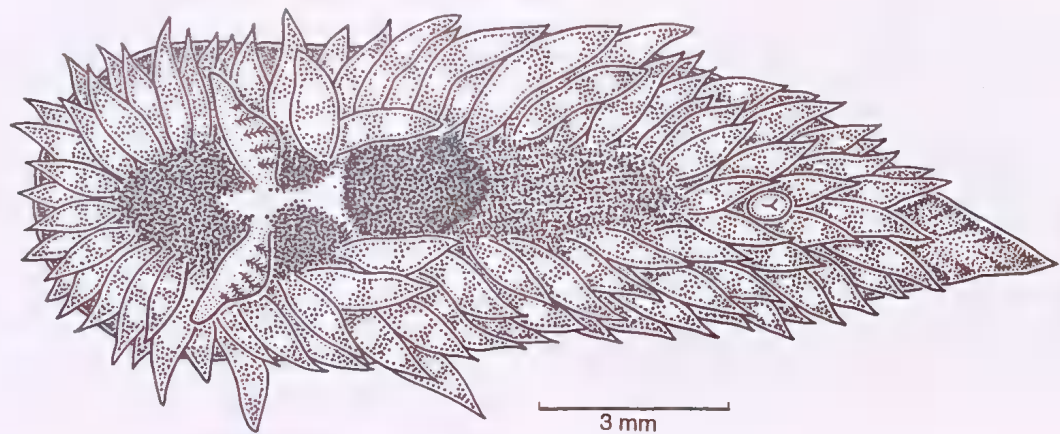


Figure 16.99 Family Zephyrinidae. *Caldukia affinis*, dorsal view. (After photograph by R.C. Willan)

[L. Newman]

The reproductive system is relatively simple with a long prostatic vas deferens, a simple and sometimes extremely long penis, a bursa copulatrix, and often a minute receptaculum seminis near the vaginal aperture. Spawn consists of an entwined mass laid on the food. Within the actual spawn mass are numerous capsules, each containing one to many eggs. Each planktotrophic larva on hatching has a coiled veliger shell.

It can be argued that the Zephyrinidae are the most advanced family of cladohepatic nudibranchs. This view is supported by several apomorphies: the tentaculate oral veil, the shape of the rhinophores, the caruncle, possession of cerata, the extension of cerata anteriorly, digestive diverticula that penetrate the cerata, the fusion of the mantle and foot, ramified digestive gland diverticula, rectal glands, and especially the mid-dorsal anal site. The only characteristic of other ceratal-bearing armininans which can be considered more highly derived, is the narrowing of the radular row though reduction of the number of teeth across a row from three in the Madrellidae to just the rachidian tooth in the Pinufiidae.

Zephyrinids feed upon ctenostomatous bryozoans. *Janolus* species eat arborescent species, such as *Bugula dentata*, *Orthoscuticella* sp. and *Bicellaria ciliata* (Miller & Willan 1986), whereas *Caldukia* species consume encrusting species like *Beania magellanica* (Morton & Miller 1968; Miller 1970). *Caldukia* species may take up to 35 minutes to detach a single zooid of *Beania* (Miller 1970). Zephyrinids are active and at least one, *Janolus ignis*, is nocturnal (Miller & Willan 1986). When disturbed, an animal will readily shed its cerata which are sticky and adhere to anything that is contacted.

The genus *Janolus* is worldwide in distribution. The known Australian species are *Janolus australis*, from the Arafura Sea, and *J. hyalinus*, from Victoria. The latter, which is also known from New Zealand, was probably transported from Europe as part of the fouling community on ships' hulls. Additional Australian species of this genus await description and comparison with the 18 presently known species. The genus *Caldukia* contains three species - *C. affinis* in cool temperate waters of south-eastern Australia, and *C. rubiginosa* and *C. albolineata* in New Zealand.

Family Pinufiidae

The small armininan, *Pinufius rebus*, first described in 1960 from the Maldive Islands, is the sole member of the Pinufiidae (Fig. 16.100; Marcus, Er. & Marcus, Ev. 1960). It has been redescribed subsequently from live material from Tanzania and northern Queensland (Rudman 1981b, 1982a).

Pinufius rebus is peculiar because of its apparent mixture of doridine, arminine and aeolidine characters. The adult length is 7 mm. The body is broadly oval and flattened, and the mantle is distinct from the foot below. An irregular, double row of cerata is

present around the edge of the mantle; some additional cerata arise from short radial ridges on the mantle, usually two per ridge. All the cerata are completely resorbed when an animal is starved for a few days (Rudman 1982a). The posterior edge of the semicircular oral veil is confluent with the narrow foot. There are no oral tentacles. The rhinophores are short, simple and non-retractile. In life, *Pinufius* is translucent white with brown mottling caused by concentrations of zooxanthellae in subepidermal digestive diverticula.

The gut consists of a muscular pharyngeal bulb containing large wing-like jaws and a single row of cuspidate (that is, the cusp is protracted beyond the lateral denticles) teeth, large oral glands, mid-central stomach receiving the three ducts of the ramifying digestive diverticula, intestine leaving the rear of the stomach, and anus which opens just to the right of the dorsal mid-line. The digestive diverticula penetrate into the cerata. The dialic reproductive system consists of follicular ovotestis, ampulla, vas deferens, discrete prostate gland, simple penis, bursa copulatrix, and nidamental gland mass. Details of reproduction and

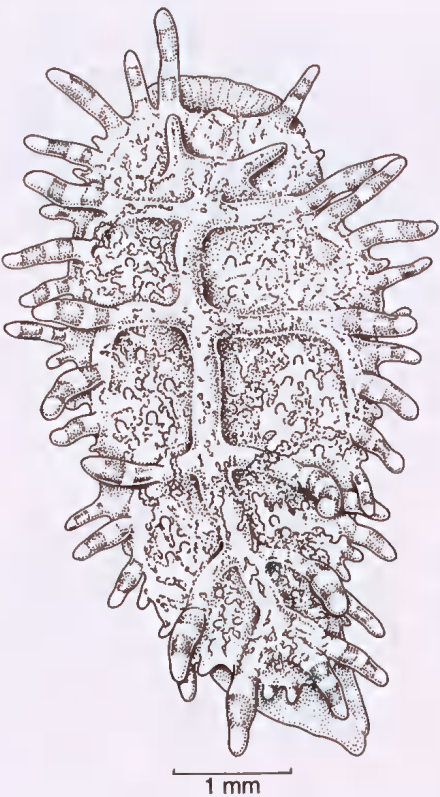


Figure 16.100 Family Pinufiidae. *Pinufius rebus*, dorsal view. (After Rudman 1981b)

[R. Plant]

development are unknown. All the morphological characters suggest that the genus *Pinufius* is highly modified and has become greatly specialised to live and feed upon *Porites* coral.

Pinufius has only ever been found on *Porites* corals. It appears to be extremely sedentary. It is cryptic, showing astonishing similarity in colour to that of its coral host; even to the extent that individuals of *Pinufius* species match the variations of colour on different sides of the same *Porites* colony (Rudman 1981b). Further knowledge of the symbiosis between *Pinufius* and its zooxanthellae must await detailed physiological experiments, but the available evidence suggests that *Pinufius* has an obligate symbiosis with the zooxanthellae it removes from its host coral. However, coral tissue is still required for normal growth and maintenance (Rudman 1982a).

Pinufius rebus probably is widely distributed in Indo-Pacific tropical waters.

Suborder AEOLIDINA

The Aeolidina are elongate nudibranchs ranging in size from 150 mm in length to less than 5 mm. They are characterised by the presence of numerous cerata, which are normally tubular but sometimes flattened and leaf-like. Each of these thin-walled, blood-filled extensions of the body cavity contains a branch of the digestive gland, which is greatly divided and generally absent from the main body cavity.

Generally, in each ceras the digestive gland branch is tubular and runs from the ceratal base to the tip where it is connected to a terminal sac, the cnidosac, which contains cnidarian stinging cells (nematocysts). The nematocysts are removed from cnidarians by the aeolid during feeding.

The cerata are arranged in regular, bilaterally symmetrical patterns along each side of the body. Their arrangement reflects the arrangement of the internal ducts from the stomach. Usually a dorsal swelling, about one-quarter of the way along the body, indicates the underlying pericardium and heart. Typically, there is a clear break between the anterior or pre-pericardial ceratal groups and the posterior or post-pericardial ceratal groups. The interval between is termed the inter-hepatic space.

The head usually has paired anterior oral tentacles and a pair of dorsal chemosensory rhinophores which always lack a basal sheath. The rhinophores vary greatly in shape, from simple, smooth tentacular processes to complex structures bearing lamellate or papillate clubs which greatly increase the sensory areas. The eyes are situated at the base of the rhinophores. There are no gills, and gas exchange takes place across the surface of the cerata and the thin body wall.

The reproductive openings are always in the right anterior quarter beneath the cerata. The anus and renal openings are usually on the right anterior side, but in some cases the anus is situated amongst, or even just above, the cerata. The position of the anus was used previously to divide aeolids into superfamilies. The three superfamilies were determined by the anus opening on the right side either below the ceratal rows (Pleuroprocta), in the inter-hepatic space alongside the heart (Acleioprocta), or among the cerata behind the inter-hepatic space (Cleioprocta). It is now generally considered that ceratal arrangement and the position of the anus are not good indicators of phylogenetic relationships.

The buccal bulb is usually surrounded by a pair of large chitinous jaw plates. The radular formula is usually 0.1.0 and sometimes 1.1.1. In a few forms there are more lateral teeth, a condition considered primitive.

Most species feed on cnidarians. Predators on zoantharians (anemones) and hydrozoans (hydroids) (Rudman 1981a) utilise the nematocysts from these for their own defence. Other species which feed on scleractinian corals (Rudman 1979, 1981b, 1982c) and alcyonaceans (Rudman 1981c, 1991b) do not use the (apparently ineffective) nematocysts from their food defensively, and rely

instead on glandular secretions from the ceratal epithelium. A few aeolids do not feed on cnidarians. Species in the genus *Favorinus* feed on opisthobranch eggs and *Fiona pinnata* prey on goose barnacles. Although most species are benthic, some are pelagic or live exclusively on floating objects in the sea.

Aeolid classification has been based on the way the cerata are arranged, whether in rows, arches or combinations of rows and arches (Odhner 1934, 1939; Burn 1962b, 1966c, 1966d). In most species the cerata insert directly into the body wall; in some species rows of cerata are arranged on raised brackets or ridges. As is discussed under individual families, the reliance on ceratal arrangement is now being questioned by some taxonomists (for example, Miller 1971, 1974, 1977), but at present there is no general agreement on what group of characters should be used in aeolid taxonomy and phylogeny. Like many other opisthobranch groups there is evidence of much convergent evolution (Rudman 1980, 1981c, 1982a, 1990b, 1991b; Gosliner & Ghiselin 1984), and until the anatomy and functional morphology of a greater range of species is investigated the phylogeny of aeolids must remain uncertain.

Family Flabellinidae

A family of small to large elongate aeolids, up to 75 mm long, flabellinids are often brightly coloured (Pl. 37.1) and are usually found on colonies of hydroids upon which they feed.

The body is usually long, narrow and tapering, and relatively deep (Fig. 16.101A). A ridge or mantle brim sometimes present along the body separates the dorsum from each side. This ridge is a remnant of the mantle skirt found in other nudibranch groups, such as the Eudoridoidea. The cerata are usually arranged in single rows or clusters of rows down each side of the body (Fig. 16.101A). In some species, the cerata insert individually into the body; in others, each row of cerata is mounted on a low oblique mound or rarely on raised prominent basal lobes or flanges.

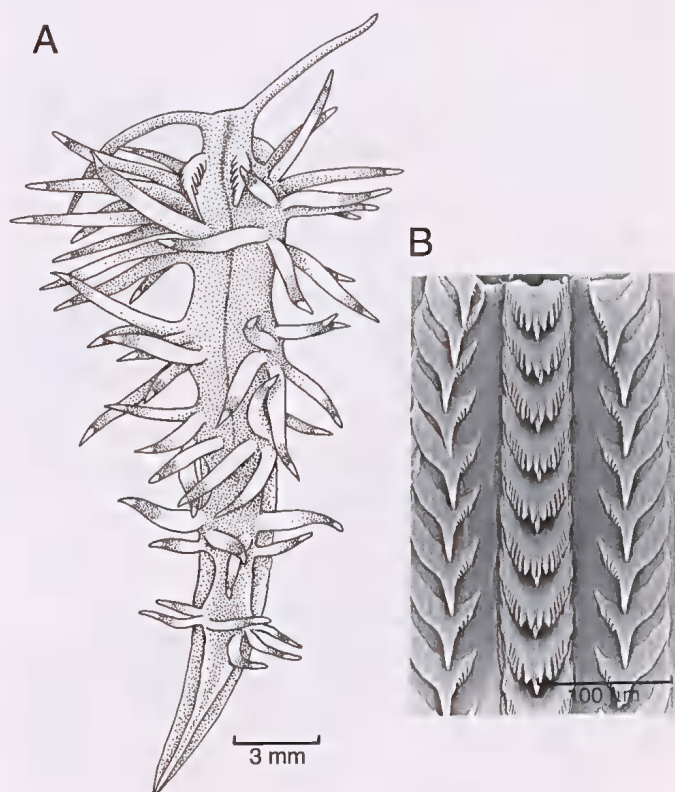


Figure 16.101 Family Flabellinidae. *Flabellina rubrolineata*: A, animal, dorsal view; B, section of the triseriate radula which is characteristic of the family. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

16. OPISTHOBRANCHIA

The rhinophores are either simple, smooth, tapering rods or elaborated with papillate or lamellate clubs. The oral tentacles are usually long and tapering with a broad triangular base. The foot is usually broad and the anterior corners are tentaculiform.

The anus opens on the right side either below the ceratal rows (pleuroproctic) or in the inter-hepatic space (acleioproctic).

The radula is triserial (formula: 1.1.1; Fig. 16.101B). The cusp of the central tooth is flanked with denticles, and the lateral teeth are normally denticulate along the inside edge. Usually, the jaw plates bear two or three rows of irregular 'teeth' or 'denticles' along the cutting edge. Large composite oral glands, found on each side of the oesophagus, open ventrally near the mouth through a common duct.

Recently, many authors have considered the two largest 'genera', *Flabellina* and *Coryphella*, to form one genus (Gosliner & Griffiths 1991; Gosliner & Willan 1991), as anatomy of the type species of each genus represents stages in a continuum. Species attributable to *Flabellina* and/or *Coryphella* are found throughout Australian waters. Some of these are endemic to temperate Australia, and others, from warmer waters, occur throughout the Indo-West Pacific. The genus *Tularia*, known only from temperate Australia and New Zealand, is considered to be a member of this family (Miller 1971). In the only known species, the cerata are borne on bracket-like lobes and the lateral radular teeth are shaped like a parallelogram with a non-denticulate cusp on the upper inside corner.

Available information suggests that most species of this family feed on hydroids. In an interesting study of six species of *Coryphella* in the Gulf of Maine, Kuzirian (1979) reported that most species prefer hydroids *Tubularia* and *Eudendrium* but are able to diversify their choice of hydroid food if these genera are scarce. *Coryphella salmonacea*, which breeds through the winter months when hydroids are scarce, feeds on ascidians as an adult. The different species also exhibit a range of life cycles and development types.

Family Eubranchidae

Members of the Eubranchidae are small aeolids, usually less than 10 mm long, with relatively long, smooth rhinophores and short oral tentacles (Fig. 16.102A). The few cerata are usually arranged in simple rows. Usually the cerata are inflated (Pl. 36.2), sometimes with a median constriction, and there may be one or more rings of tubercles around the circumference. The anus opens on the right side of the body in the inter-hepatic space (acleioproctic), immediately behind the renal pore (Miller 1971).

The foot is usually slightly wider than the body and its anterior corners may be rounded, angular or tentaculiform.

The radula is triserial (formula 1.1.1; Fig. 16.102B). The central tooth has four or five large denticles on each side of a pointed central cusp. Each lateral tooth has a wide base, sometimes three or four times the width of the central tooth, and a non-denticulate

pointed cusp near the inner side of the tooth. The masticatory border of the jaw plates either has a single row of teeth or is smooth. Large oral glands are situated on each side of the oesophagus just behind the buccal bulb.

These small aeolids are often found in large numbers on small gymnoblastic and calyptoblastic colonial hydroids. Few species are known from Australian waters (Burn 1964b) but it is probable that there are many species yet to be found. The ecology and life history of European species have been reviewed by Thompson & Brown (1984).

Family Aeolidiidae

Aeolidiid species are slow-moving, small to large animals reaching up to 120 mm in length (Fig. 16.103A, B). The elongate body may be broad or narrow, and the foot is slightly wider than the body. The oral tentacles are usually well developed and the anterior corners of the foot are angular or tentacular. The rhinophores may be simple and smooth, or complex structures with papillate or lamellate clubs.

The cerata, often numerous and crowded, are usually arranged in rows which are sometimes raised on a common ridge. In some genera, the cerata are less numerous and their arrangement is more obscure. In some species the cerata are cylindrical and tapering, but in others they are flattened and liable to be cast off by the animal when disturbed.

Large oral glands are usually present and the anus opens behind the inter-hepatic space (cleioproctic). Each tooth in the uniserial radula (formula 0.1.0) has a broad basal arch and numerous crowded denticles (Fig. 16.103C–E). In some genera, the teeth show no distinct central cusp, and in others the central cusp is reduced and sunken and the lateral denticles are arranged in a large secondary arch on each side.

Most species feed on sea anemones. Thompson & Brown (1984) reviewed the many studies that have been published on the feeding behaviour and food preferences of the large Northern Hemisphere species *Aeolidia papillosa*. *Aeolidiella foulisi*, common intertidally throughout Australia, feeds on small intertidal anemones including *Actinia tenebrosa* and *Anthothoe albocincta* (W.B. Rudman personal observation). The larger *Spurilla australis* is often found on large laminarian algae, where it preys on the small mobile anemone *Cricophorus nutrix* (Morton & Miller 1968; W.B. Rudman personal observation). In tropical waters, *Aeolidiopsis harrietae* and *Aeolidiopsis ransonii* feed on the colonial zoantharian *Palythoa* (Rudman 1982a). Species of *Cerberilla* are modified for burrowing through sand and are seldom seen alive although they are apparently not uncommon. One species, *Cerberilla incola*, is common in sediment samples from Jervis Bay and Botany Bay in south-eastern Australia.

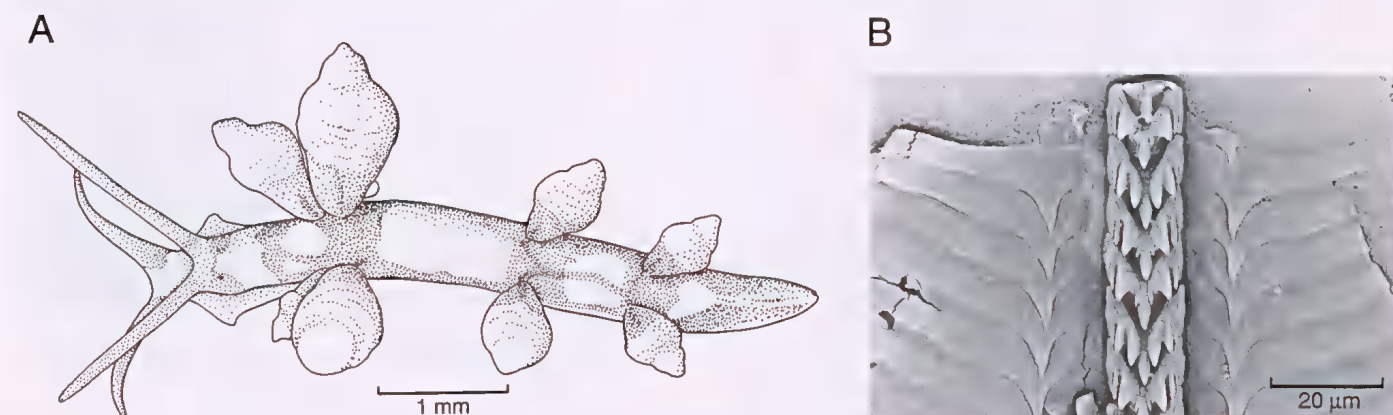


Figure 16.102 Family Eubranchidae. A, *Eubranchus inabai*, dorsal view. B, section of the triserial radula of a *Eubranchus* sp.; the eubranchid radula differs from those of flabellinids in having broad lateral plates. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

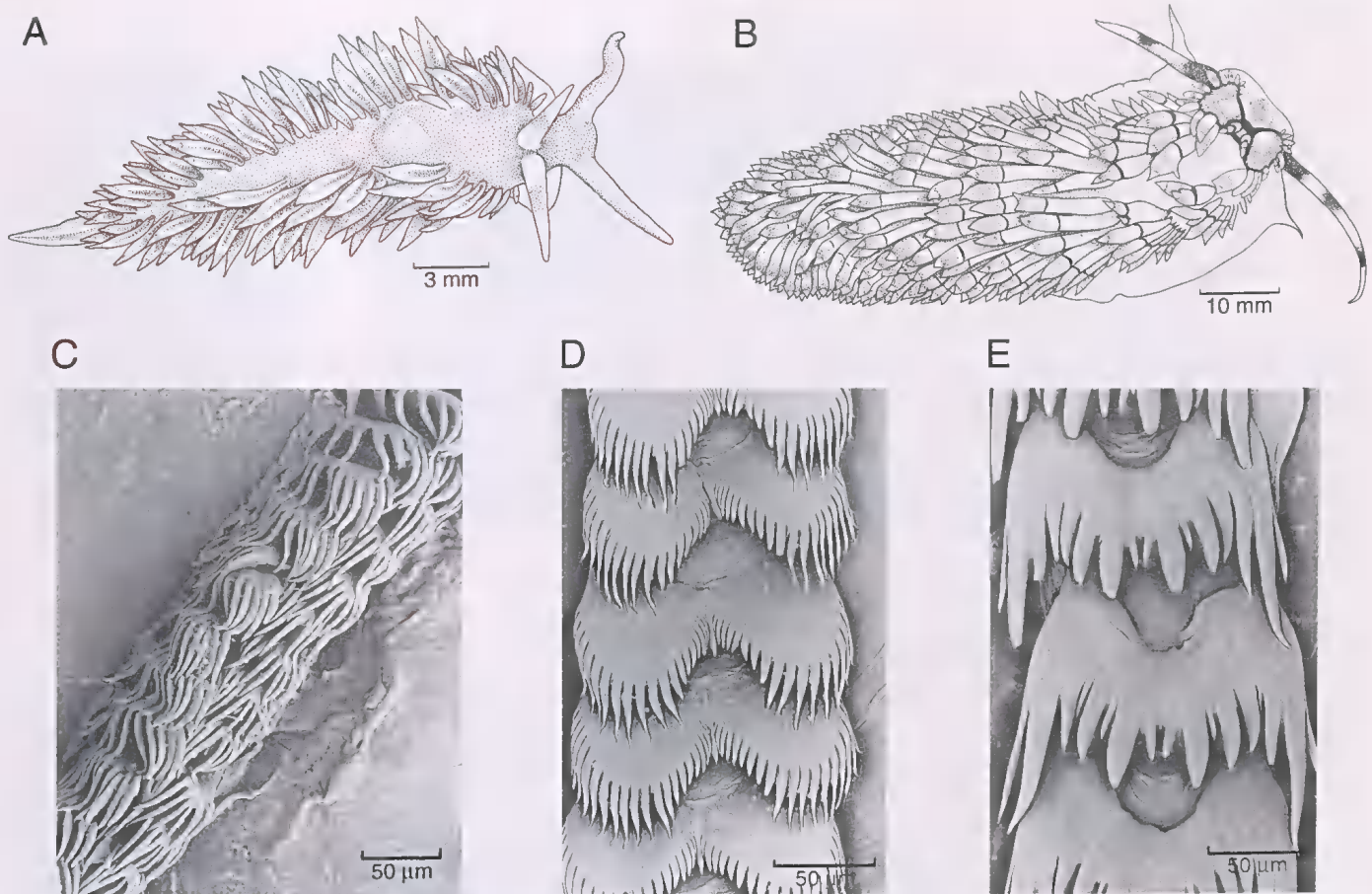


Figure 16.103 Family Aeolidiidae. A, *Aeolidiella foulisi*, dorsal view. B, *Cerberilla affinis*, dorsal view. C–E, sections of radulae: C, *Protaeolidiella atra*; D, *Aeolidiella foulisi*; E, *Cerberilla incola*. (A, B, after photographs by W.B. Rudman) [A, B, S. Weidland; C–E, G. Averm]

Many species of this family illustrate trends in the evolution of a symbiosis with zooxanthellae, the unicellular plant-like dinoflagellates, that are common symbionts with cnidarians (Rudman 1982a). The zooxanthellae are ingested by the aeolid while feeding on anemones and, instead of being digested with the cnidarian tissue, are moved to special branches of the digestive gland within the body wall. The zooxanthellae are nurtured in the aeolid tissue and photosynthetic products produced by them are removed by the aeolid for its own nutrition. Species with zooxanthellae are usually recognisable by brown reticulations in the body wall and often the development of flattened cerata which are liable to be cast when the animal is disturbed.

Family Glaucidae

The Glaucidae are small to large aeolids (5–120 mm) and are well represented in Australian waters. They are usually narrow and deep with a long tapering tail, and are often described as 'pugnacious' or 'aggressive' (Fig. 16.104A–E).

A ridge often separates the back from the sides and the oral tentacles are long and tapering. The rhinophores may be simple, annulate, papillate or lamellate and the cerata are arranged in rows, sometimes clusters of rows, or in arches. The various combinations of these ceratal arrangements in single or multiple rows and arches are used to define the subfamilies. The value of this character set is somewhat doubtful, for it is possible that the different ceratal arrangements have arisen independently many times, as has been shown in the genus *Phyllodesmium* (Rudman 1981c). The anus is usually situated within the cerata behind the inter-hepatic space (cleioproctic).

The oral glands are simple and the radula is uniseriate (Fig. 16.105A–F). Usually the radular teeth have long basal limbs and a large pointed cusp which is flanked by several prominent denticles. Modifications to this form occur in *Phyllodesmium* (Fig. 16.105C, D) and *Favorinus* (Fig. 16.105B), two genera with specialised feeding behaviour.

There is much dispute concerning the relationships within this group of aeolids. Some authors follow Miller (1974), who treated many previously accepted families as subfamilies, whereas others have taken a more conservative view. In the absence of any agreed classification it is appropriate to consider separately some of the genera and the subfamilies they represent.

The genus *Phidiana* (= ? *Facelina*) (subfamily Facelininae; Figs 16.104A, 16.105A) includes medium-sized to small aeolids up to 40 mm long. The cerata are usually arranged in a large group of rows in front of the pericardium and single spaced rows behind (Pl. 36.4). They feed on hydroids.

The genera *Favorinus*, *Phyllodesmium*, *Austreaolis* and *Godiva* (subfamily Favorininae; Figs 16.104B, 16.105B–E) include numerous large to medium-sized aeolids, up to 120 mm long, in which the cerata are arranged in arches comprising either single or multiple rows of cerata. Ecologically this is the most diverse of the subfamilies of the Glaucidae. Although most feed on hydroids, all the known species of the genus *Phyllodesmium* feed on alcyonacean soft corals or gorgonians. The variety of ceratal arrangements within the genus reflects adaptation by many species to symbioses with zooxanthellae removed from the soft corals upon which they feed (Rudman 1981c, 1991b). *Phyllodesmium* and *Favorinus* are the only two genera in the family which lack cnidosacs for nematocyst storage in the tips of their cerata. The nematocysts from the food alcyonaceans of *Phyllodesmium* are too small to be adequate for defence; and *Favorinus* species feed on the eggs of other opisthobranchs and, rarely, on the eggs of caenogastropods. In both genera the radular tooth has been greatly modified; its central, very elongate cusp lacks denticles or they are very reduced. *Austreaolis* and most other favorine aeolids are relatively large and active, and feed on hydroids. Often when disturbed they will bristle their cerata, and point the tips containing the cnidosacs at the source of the disturbance (Rudman 1980; Willan 1987b).

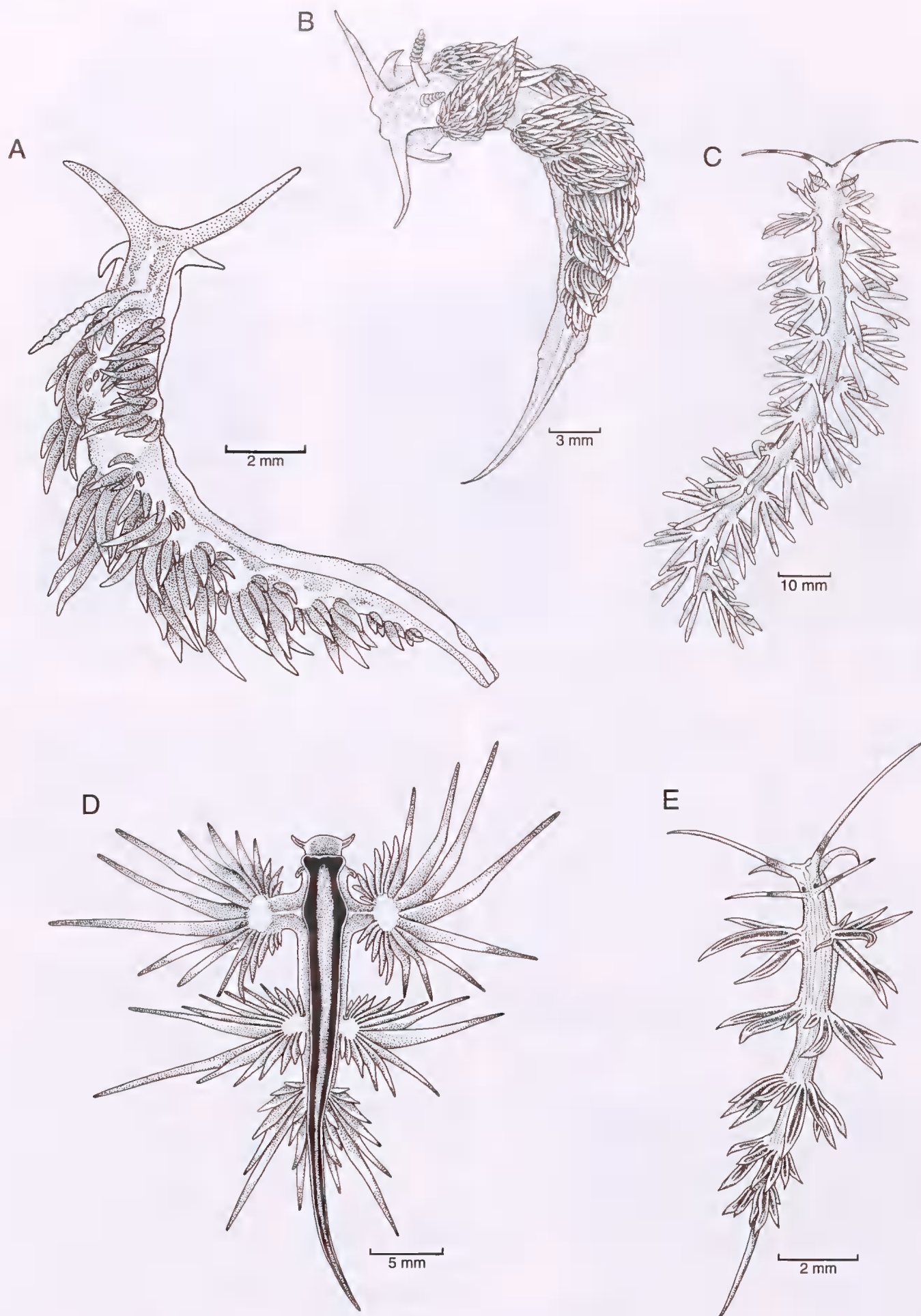


Figure 16.104 Family Glaucidae. A, subfamily Facelininae, *Phidiana newcombi*, dorsal view. B, subfamily Favorininae, *Austraeolis cacaotica*, dorsal view. C, subfamily Pteraeolidiinae, *Pteraeolidia ianthina*, dorsal view. D, subfamily Glaucinae, *Glaucus atlanticus*, dorsal view. E, subfamily Cratena subfamily, *Cratena lineata*, dorsal view. (After photographs by W.B. Rudman)

[S. Weidland]

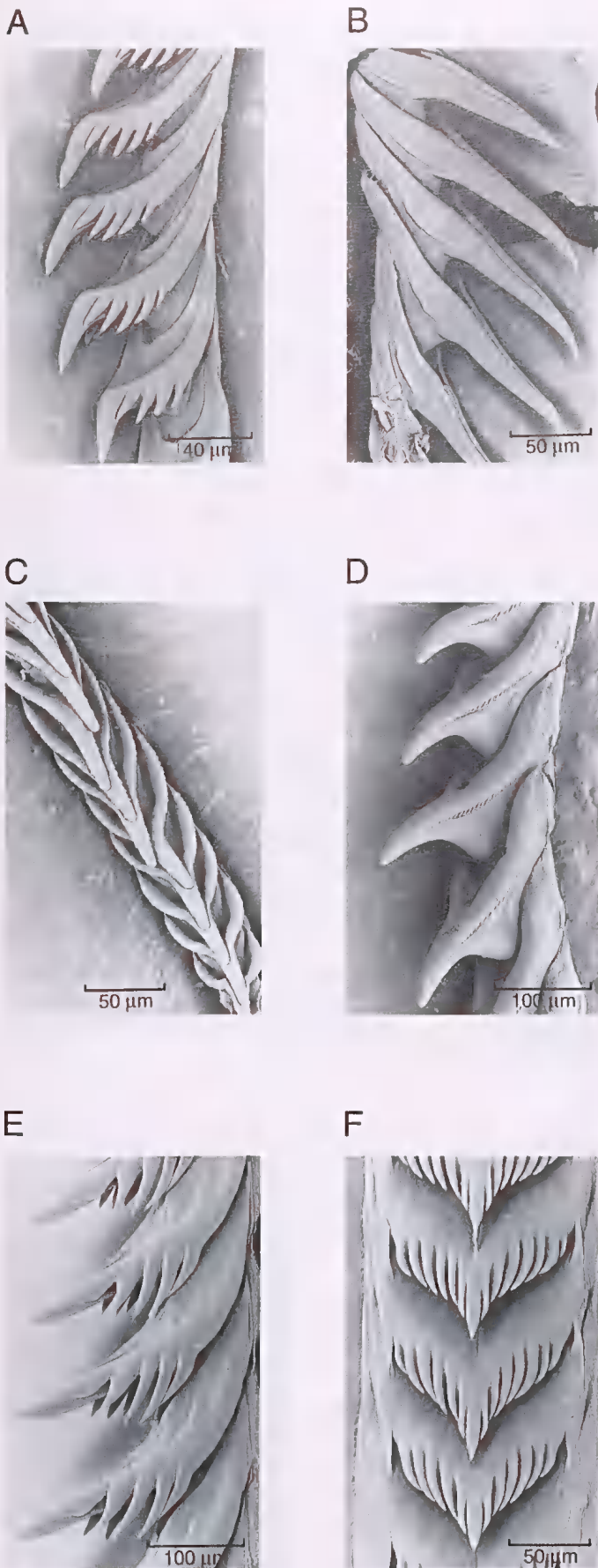


Figure 16.105 Family Glaucidae, sections of radulae. **A**, subfamily Facelininae, *Phidiana newcombi*. **B–E**, subfamily Favorininae: **B**, *Favorinus japonicus*, single row of smooth, knife-like teeth characteristic of this egg-feeding genus; **C**, *Phyllodesmium briareum*, single row of elongate and denticulate radular teeth characteristic of these soft coral feeders; **D**, *Phyllodesmium serratum*, dorso-lateral view of radula; **E**, *Godiva* sp. lateral view of radular teeth, typical of hydroid-feeding favorinids. **F**, subfamily Pteraeolidiinae, *Pteraeolidia ianthina*. [G. Avern]

The monotypic subfamily, Pteraeolidiinae (Figs 16.104C, 16.105F), contains the genus *Pteraeolidia* and possibly two species. The animals are extremely elongate and the cerata are arranged on flap-like extensions down each side of the body. They may attain 150 mm in length. The increased body length and fan-like clustering of the cerata appear to be adaptations to increase the surface area exposed to light, for *Pteraeolidia* also has symbiotic zooxanthellae in its tissues (Rudman 1982a, 1986a, 1987a; Hoegh-Guldberg & Hinde 1986; Hoegh-Guldberg *et al.* 1986). Willan (1989) describes feeding and antagonistic behaviour in this genus.

Glaucus and *Glaucilla*, which form the subfamily Glaucinae (Fig. 16.104D), are two monotypic genera of remarkable pelagic nudibranchs in which the cerata are arranged in a few either single or multiple-rowed arches. The arches, never more than three or four on each side, are on large lateral swellings. The rhinophores and oral tentacles are very reduced. The animals spend their lives floating upside down buoyed by a bubble of gas in their stomach. They feed exclusively on *Physalia* (Portuguese man-o'-war or blue-bottle) and other colonial floating cnidarians such as *Velella* and *Porpita*, and as with most other aeolids, store the nematocysts from their prey in the tips of the cerata (Thompson & Bennett 1969, 1970).

Cratena (subfamily Crateninae; Fig. 16.104E) and *Herviella* (subfamily Herviellinae) are two genera of smaller glaucids (5–20 mm long) with similar habits to *Phidiana*. In *Cratena*, the first, pre-cardiac, group of cerata form a single arch whereas the post-cardiac cerata are arranged in single rows. All the cerata of *Herviella* are in single rows, with only one pre-cardiac row (Rudman 1980; Burn 1967c).

Family Embletoniidae

Embletoniids are small and often very elongate. They are characterised by the large, bilobed oral veil, the loss of oral tentacles and the single row of large tubular cerata along each side of the body (Fig. 16.106A).

Generally the family has been considered to be aeolidinan, probably closely related to the Tergipedidae (Baba 1959b; Baba & Hamatani 1963; Gosliner & Griffiths 1981). Most authors accept a single genus, *Embletonia*. Some authors consider this small group of three, possibly four, species to be dendronotinans (Miller 1977; Willan & Coleman 1984; Miller & Willan 1991). Miller & Willan (1991) gave four reasons for considering *Embletonia* to be dendronotinans. They are: presence of dendronotinan oral veil; lack of oral tentacles; three-lobed oral gland; and lack of cnidosacs. Of these characters, the first two are really aspects of one feature. Either the head region is a dendronotinan oral veil, but lacking the characteristic ventral groove along each side, or it is a tergipedid head lacking oral tentacles. Although considering the family to be dendronotinans, Miller & Willan fail to explain the lack of sheathed rhinophores.

The three-lobed oral gland closely resembles the elaborate oral gland developed in the tergipedids, especially the coral-feeding genus *Phestilla* (Rudman 1981b). Similarly the nature of the cnidosac is open to interpretation. Although Miller & Willan referred to 'pads' described by Ev. Marcus & Er. Marcus (1958) both Baba & Hamatani (1963) and W.B. Rudman (personal observation) have observed sacs containing nematocysts at the ceratal tips.

In the European *Embletonia pulchra*, the tips of the cerata are rounded and, although a cnidosac is lacking, there are up to four terminal pads of nematocysts on each ceras. In the Indo-West Pacific species, the end of each ceras is divided twice, forming four knobs, each have a terminal sac containing nematocysts.

In all species the anus opens between the second and third cerata on the right and has been variously described as pleuroproct or acleioproct. The rhinophores are simple. Oral glands are present and the single median tooth in the uniseriate radula has a central pointed cusp flanked by a few denticles (Fig. 16.106B). The cutting edge of the jaw plates is denticulate.

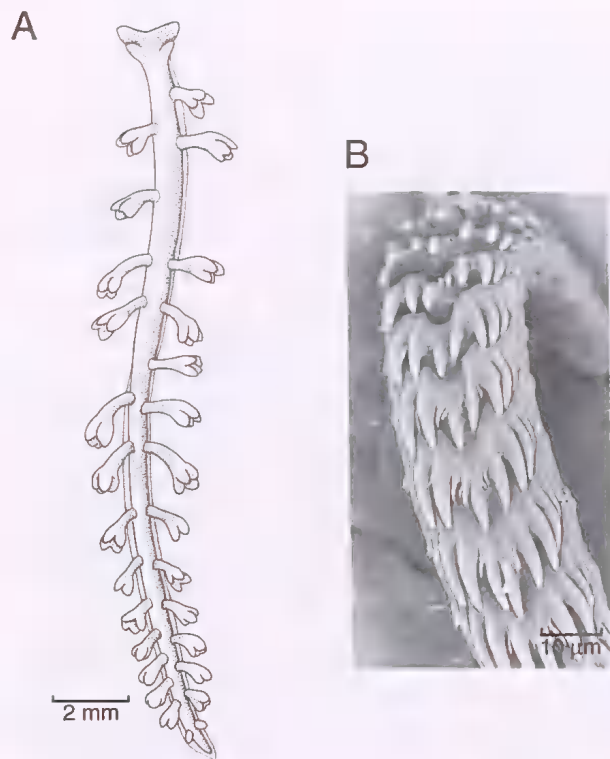


Figure 16.106 Family Embletoniidae. *Embletonia gracile*: A, animal, dorsal view; B, radula with a single row of comb-like teeth. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, G. Avern]

Most reports suggest that species feed on hydroids, although a European species is reported to sometimes feed on fish eggs (Thompson & Brown 1984).

Family Tergipedidae

Members of the Tergipedidae are usually small aeolids, often exceedingly abundant on subtidal rock walls, on temporary hydroid growths on ship's hulls, buoys or flotsam, and on the leaves of seagrasses and laminarian algae.

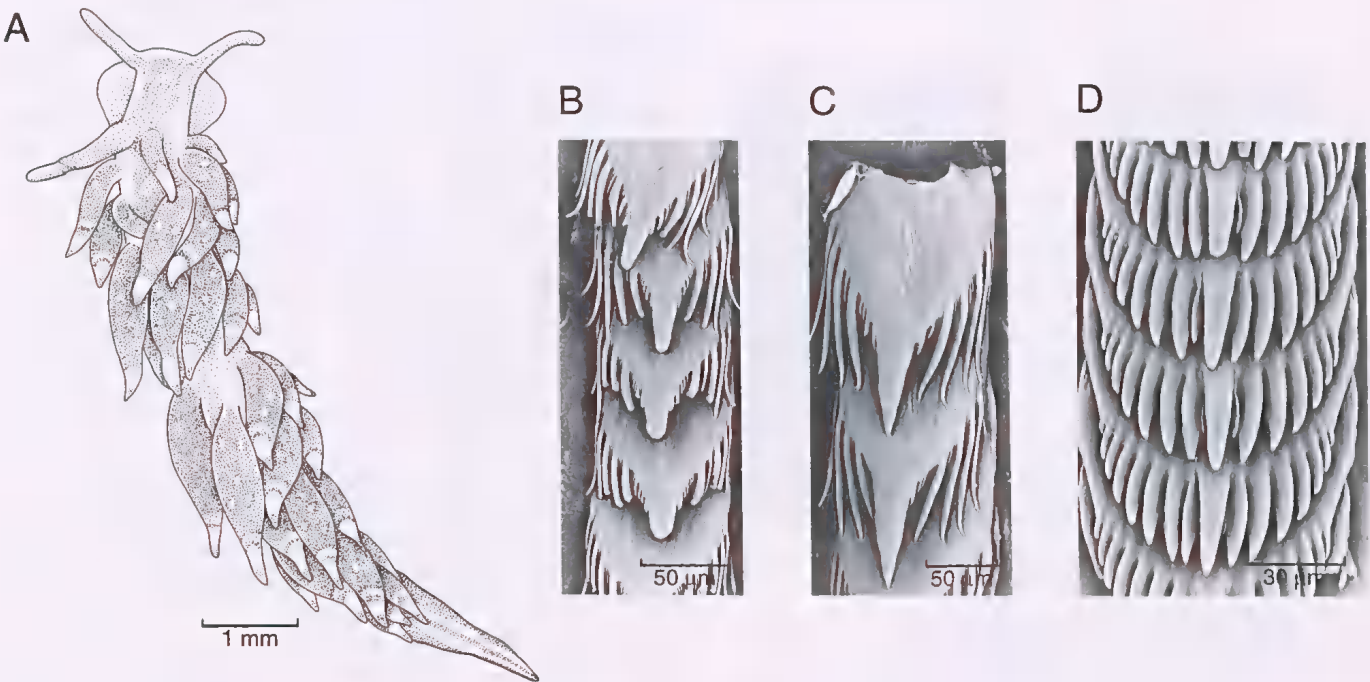


Figure 16.107 Family Tergipedidae. A, *Cuthona* sp., dorsal view. B, C, sections of radulae of *Phestilla melanobrachia* which feeds on hard coral (*Tubastraea*) and breaks the denticles and central cusps (B) probably a result of scraping tissue of the hard coral; C, teeth from an unused part of the radula. D, radula of *Cuthona sibogae*; these teeth are typical of hydroid-feeding tergipedids. (A, after photograph by W.B. Rudman) [A, S. Weidland; B–D, G. Avern]

The body is usually small with a pronounced pericardial swelling on the dorsum just behind the rhinophores. The foot is usually wider than the body, rounded at the anterior corners and often long and tapering posteriorly. The oral tentacles and longer rhinophores are usually smooth (Fig. 16.107A).

The tubular cerata are usually arranged in single oblique rows on each side of the body. There is usually more than one ceratal row in front of the pericardium. The anus is on the right side in the inter-hepatic space (acleioproct).

The oral glands are large and composite and in larger species extend some distance posteriorly in the body cavity. The jaw plates are more elongate than in other aeolid families and the cutting edge may be denticulate, smooth or with bristles. The radula is uniseriate (Fig. 16.107B–D) and usually the teeth have a central cusp, either protruding or retracted, flanked by smaller denticles on each side.

At least two genera are reported from Australia, *Cuthona* and *Phestilla*. *Cuthona* has the most representatives, reported under the names *Catriona*, *Trinchesia*, *Narraeolidia* and *Toorna* (Burn 1961, 1963b, 1964b, 1973b). They are small species of less than 5 mm in length and live on hydroids, often in large numbers (Pl. 36.3). In *Cuthona kuiteri*, which feeds on a tubularian hydroid, *Zyzyzus*, rings of secondary papillae on the cerata mimic the tentacles of the hydroid polyp (Rudman 1981a).

The genus *Phestilla* is represented in Australia by at least three species, *P. minor*, *P. lugubris* and *P. melanobrachia* (Pl. 36.1). These species are remarkable for their exclusive diets of reef-forming hard corals (Rudman 1981b), the first two on species of *Porites*, and the last on dendrophyllid corals such as *Dendrophyllia* and *Tubastraea*. In size and morphology, *Phestilla minor* is very similar to a species of *Cuthona*. However, the cnidosac at the tip of the cerata is replaced in *Phestilla* by a swollen glandular region, possibly because the nematocysts of scleractinian corals are apparently unsuitable for defence. The other two species are much larger, growing to more than 50 mm in length, and have numerous long cerata arranged in single rows on raised ridges. The radular teeth (Fig. 16.107B, C) also differ in the presence of long, slender denticles, as long or longer than the central cusp, which are used to scrape the animal tissue from the coral skeleton. The radular teeth of *C. sibogae* are comb-like in form.

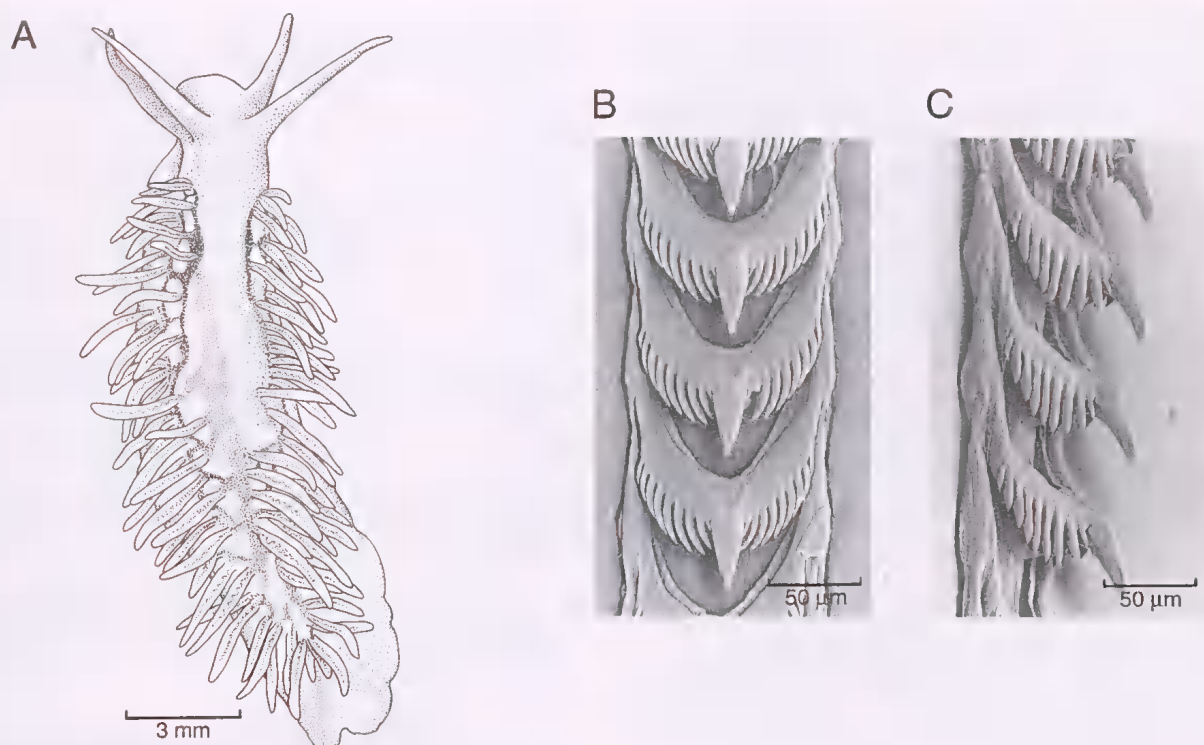


Figure 16.108 Family Fionidae. *Fiona pinnata*: A, animal, dorsal view; B, radula teeth, dorsal view; C, radula teeth, lateral view. (A, after photograph by W.B. Rudman) [A, S. Weidland; B, C, G. Avern]

As with most aeolid families, there is continuing debate on the taxonomy of the group, with many generic names proposed to accommodate each new combination of anatomical characters discovered. Miller (1977) proposed suppressing most of the earlier names in *Cuthona*. Although this has not met with universal acceptance most workers are following his proposals. Australian species have been placed in the genera listed above.

Family Fionidae

The family is named for the single species, *Fiona pinnata* (Fig. 16.108), which has a worldwide distribution, and was first recorded from Australia by Burn (1967d). It grows to about 20 mm in length and lives exclusively on floating objects in the sea, usually feeding on goose barnacles (*Lepas* spp.), but sometimes on hydrozoan cnidarians (M.C. Miller personal observation), including the floats of the pelagic colonial *Physalia* and *Velella*. Willan (1979b) reviewed the Fionidae.

The body is elongate and the rhinophores and oral tentacles are smooth. The numerous cerata are arranged irregularly along each

side of the body, without any clear clustering or obvious system of rows. The cerata are unique in having a broad, undulating, postero-dorsal membrane along their length. Cnidosacs are absent. The anus opens latero-dorsally on the upper fringe of the cerata on the right side.

Oral glands are well developed and the jaw plates are very elongate. The radula is uniseriate; the teeth have a broad arch-like base and a prominent pointed cusp flanked with a group of denticles on each side (Fig. 16.108B, C).

Although often described as pelagic (Burn 1967d) this is not strictly correct, for after settling upon floating objects at metamorphosis, *Fiona* is unable to swim. Settling and metamorphosis usually take place on goose barnacles which are themselves attached to floating objects (Holleman 1972), or on the floats of siphonophores and chondrophores such as *Physalia* and *Velella* (Bayer 1963). Large numbers of *Fiona* and their egg masses are often found on goose barnacles attached to driftwood, fishing-floats, sepions of *Sepia* or the shells of *Spirula* washed up on beaches after storms.

LITERATURE CITED

- Abbott, R.T. (1974). *American Seashells*. Van Nostrand Reinhold : New York 2nd edn. 663 pp.
- Aboul-Ela, I.A. (1959). On the food of nudibranchs. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 117: 439–442
- Abraham, P.S. (1876). Notes on some genera of nudibranchiate Mollusca, with notices of a new genus and some hitherto undescribed species in the collection of the British Museum. *Annals and Magazine of Natural History* (4)18: 132–146
- Abraham, P.S. (1877). Revision of the anthobranchiate nudibranchiate Mollusca, with descriptions or notices of forty-one hitherto undescribed species. *Proceedings of the Zoological Society of London* 1877: 196–269
- Adams, H. & Adams, A. (1854). *The genera of Recent Mollusca, arranged according to their organization*. Vol. 2. Van Voorst : London 92 pp.
- Alder, J. (1848). A catalogue of the Mollusca of Northumberland and Durham. *Transactions of the Tyneside Naturalists' Field Club* 1: 97–209
- Alder, J. & Hancock, A. (1855). Part 7. *Monograph of the British Nudibranchiate Mollusca*. Fam. 1, pls 21A & 27; Fam. 2, pls 1 & 2; Fam. 3, pls 38A, 45–48; Appendix pp. I–XXVIII
- Alder, J. & Hancock, A. (1864). Notice of a collection of nudibranchiate mollusca made in India by Walter Elliot, Esq., with descriptions of several new genera and species. *Transactions of the Zoological Society of London* 5: 113–147
- Allan, J.K. (1932). Sea-hares. *Australian Museum Magazine* 4: 419–425
- Allan, J.K. (1933). Opisthobranchs from Australia. *Records of the Australian Museum* 18: 443–450
- Allan, J.K. (1941). Australian sea-hares and tailed sea slugs. *Victorian Naturalist* 57: 178–182

16. OPISTHOBRANCHIA

- Allan, J.K. (1950). *Australian Shells: with related animals living in the sea, in freshwater and on the land*. Georgian House : Melbourne xix 470 pp.
- Aldredge, A.L. (1972). Abandoned larvacean houses: A unique food source in the pelagic environment. *Science* 177: 885–887
- Angas, G.F. (1864). Description d'espèces nouvelles appartenant à plusieurs genres de Mollusques nudibranches des environs de Port Jackson, (Nouvelles-Galles du Sud), accompagnée de dessins faits d'après nature. *Journal de Conchyliologie* 12: 43–70
- Angas, G.F. (1867). Descriptions of thirty-two new species of marine shells from the coast of New South Wales. *Proceedings of the Zoological Society of London* 1867: 110–117
- Annandale, T.N. (1924). Gastropoda. Pp. 27–49 in Annandale, T.N. & Prasad, B. Report on a small collection of molluscs from the Chekiang Province of China. *Proceedings of the Malacological Society of London* 16: 27–49
- Annandale, T.N. & Prasad, B. (1919). Some gastropod molluscs from the Gangetic Delta. *Records of the Indian Museum* 16: 241–258
- Archer, M. & Clayton, G. (eds) (1984). *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle, Western Australia 1203 pp.
- Arnaud, P.M., Poizat, C. & Salvini-Plawen, L. von (1986). Marine interstitial Gastropoda (including one freshwater interstitial species). Pp. 153–176 in Botosaneanu, L. (ed.) *Stygo fauna mundi*. E.J. Brill : Leiden
- Audesirk, T.E. & Audesirk, G.J. (1977). Chemoreception in *Aplysia californica*. – II. Electro-physiological evidence for detection of the odor of conspecifics. *Comparative Biochemistry and Physiology* 56A: 267–270
- Baba, K. (1930). Studies in Japanese nudibranchs. (2) A. Polyceridae, B. *Okadaia* n.g. preliminary report. *Venus* 2: 43–50
- Baba, K. (1931). A noteworthy gill-less holohepatic nudibranch, *Okadaia elegans* Baba, with reference to its internal anatomy. *Annotationes Zoologicae Japonenses* 13: 63–89
- Baba, K. (1937a). Contribution to the knowledge of a nudibranch *Okadaia elegans* Baba. *Japanese Journal of Zoology* 7: 147–190
- Baba, K. (1937b). Two new species of the nudibranchiate genus *Notobryon* from Sagami Bay, Japan. *Venus* 7: 165–170
- Baba, K. (1949). *Opisthobranchia of Sagami Bay collected by His Majesty the Emperor of Japan*. Iwanami Shoten : Tokyo 194 pp. 50 pls
- Baba, K. (1954). *Runcina setoensis*, a new and rare species from the coast of Kii, Middle Japan (Opisthobranchia). *Publications of the Seto Marine Biological Laboratory* 3: 373–374
- Baba, K. (1955). *Opisthobranchia of Sagami Bay collected by His Majesty the Emperor of Japan. Supplement*. Iwanami Shoten : Tokyo 59 pp.
- Baba, K. (1957). The species of the genus *Elysia* from Japan. *Publications of the Seto Marine Biological Laboratory* 6: 69–74
- Baba, K. (1959a). The family Stiligeridae from Japan (Opisthobranchia – Sacoglossa). *Publications of the Seto Marine Biological Laboratory* 7: 327–334
- Baba, K. (1959b). A new record of an interesting species, *Embletonia gracile* Risbec, from Japan (Nudibranchia – Eolidacea). *Publications of the Seto Marine Biological Laboratory* 7: 335–336
- Baba, K. (1960). The genera *Okenia*, *Goniodoridella* and *Goniodoris* from Japan (Nudibranchia-Goniodorididae). *Publications of the Seto Marine Biological Laboratory* 8: 79–83
- Baba, K. (1961). On the identification and the affinity of *Tamanovalva limax*, a bivalved sacoglossan mollusc from Japan. *Publications of the Seto Marine Biological Laboratory* 9: 37–62
- Baba, K. (1966). Gross anatomy of the specimens of the shelled sacoglossan *Volvatella* (= *Arthessa*) collected from Okino-Erabu Island, southern Kyushu, Japan (Nudibranchia). *Publications of the Seto Marine Biological Laboratory* 14: 197–205
- Baba, K. (1967). Supplementary notes on the anatomy of *Metaruncina setoensis* (Baba, 1954) (N.G.) (Opisthobranchia – Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* 15: 185–197
- Baba, K. (1971). Anatomical studies on three species of *Doto* (*D. bella*, *D. japonica*, *D. pita*) from Japan (Nudibranchia: Dendronotoidea: Dotidae). *Publications of the Seto Marine Biological Laboratory* 19: 73–80
- Baba, K. (1976). Two new species and five common or rare species of the genus *Dermatobranchus* from Japan. *The Veliger* 19: 4–12
- Baba, K. (1985). Anatomical review of a cephalaspidean mollusk, *Nakamigawaia spiralis* Kurdoa & Habe in Habe 1961, (Aglajidae), from Japan. *Special Publication of the Mukaishima Marine Biological Station* 1985: 1–5
- Baba, K. (1990). Two small species of *Philine* new to Japan (Cephalaspidea: Philinidae). *Venus* 49: 181–187
- Baba, K. & Hamatani, I. (1959). The direct development in *Runcina setoensis* Baba (Opisthobranchia–Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* 7: 281–290
- Baba, K. & Hamatani, I. (1963). Anatomy of *Embletonia gracilis paucipillata* n. ssp. from Osaka Bay, Japan (Nudibranchia–Eolidoidea). *Publications of the Seto Marine Biological Laboratory* 11: 399–402
- Baba, K. & Hamatani, I. (1971). Record of *Phyllobranchillus orientalis* (Kelaart, 1858) (syn. *Branchophyllum orientale* var *sagamiense* Baba, 1955) from Cape Shiono-Misaki, Kii, Middle Japan (Opisthobranchia: Sacoglossa). *Publications of the Seto Marine Biological Laboratory* 19: 197–201
- Baba, K., Hamatani, I. & Hisai, K. (1956). Observations on the spawning habits of some of the Japanese Opisthobranchia. *Publications of the Seto Marine Biological Laboratory* 5: 209–220
- Baba, K. & Tokioka, T. (1965). Two more new species of *Gastropoda* from Japan, with further notes on *G. flavum* T. & B. (Gasterpoda: Opisthobranchia). *Publications of the Seto Marine Biological Laboratory* 12: 363–378
- Baluk, W. & Jakubowski, G. (1968). *Berthelinia krachi* n.sp., a bivalved gastropod from the Miocene of Poland. *Acta Palaeontologica Polonica* 13: 291–302
- Basedow, H. & Hedley, C. (1905). South Australian nudibranchs, and an enumeration of the known Australian species. *Transactions and Proceedings of the Royal Society of South Australia* 29: 134–160
- Bayer, F.M. (1963). Observations on pelagic mollusks associated with the siphonophores *Veleva* and *Physalia*. *Bulletin of Marine Science of the Gulf and Caribbean* 13: 454–466
- Bazas, M.A. & Carle, K.J. (1979). Predators of Foraminifera in the Indian River, Florida. *Journal of Foraminiferal Research* 9: 336–340
- Bebbington, A. (1977). Aplysiid species from eastern Australia with notes on the Pacific Ocean Aplysiomorpha (Gastropoda: Opisthobranchia). *Transactions of the Zoological Society of London* 34: 87–147
- Bebbington, A. & Hughes, G.M. (1973). Locomotion in *Aplysia* (Gastropoda: Opisthobranchia). *Proceedings of the Malacological Society of London* 40: 399–405
- Beeman, R.D. (1977). Gastropoda: Opisthobranchia. Pp. 115–179 in Giese, A.C. & Pearse, J.S. (eds) *Reproduction of Marine Invertebrates*. Vol. 4. Academic Press : New York
- Beeman, R.D. & Williams, G.C. (1980). Opisthobranchia and Pulmonata: the sea slugs and allies. Pp. 308–354 in Morris, R.H., Abbott, D.P. & Haderlie, E.C. (eds) *Intertidal Invertebrates of California*. Stanford University Press : Stanford
- Behrens, D.W. (1980). *Pacific Coast Nudibranchs. A guide to the opisthobranchs of the northeastern Pacific*. Sea Challengers : Los Osos, California 112 pp.
- Berger, W.H. (1978). Deep-sea carbonate: Pteropod distribution and aragonite compensation depth. *Deep-Sea Research* 25: 447–452
- Bergh, R. (1870). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 2(1): 1–30

- Bergh, R. (1871–1873). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 2(2–5): 48–246
- Bergh, R. (1876). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 2(10): 377–427
- Bergh, R. (1879). Beiträge zu einer Monographie der Polyceraden. 1. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien* 29: 599–632
- Bergh, R. (1880). Beiträge zu einer Monographie der Polyceraden. 2. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien* 30: 629–668
- Bergh, R. (1883). Beiträge zu einer Monographie der Polyceraden. 3. *Verhandlungen der königlich-kaiserlich Zoologisch-botanischen Gesellschaft in Wien* 33: 135–180
- Bergh, R. (1887). Die van Hasselt'schen Nudibranchien. *Notes from Leyden Museum* 9: 303–323
- Bergh, R. (1888a). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 2(16i): 755–814
- Bergh, R. (1888b). Die Pleuroleutiden, eine Familie der nudibranchiaten Gaströpoden. *Zoologische Jahrbücher, Abtheilung für Systematik Geographie und Biologie der Thiere* 3: 348–364
- Bergh, R. (1892). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 2(18): 995–1168
- Bergh, R. (1893a). Die Gruppe der Doridiiden. *Mittheilungen aus der Zoologischen Station zu Neapel, Zugleich ein Repertorium für Mittelmeerkunde* 6: 107–135
- Bergh, R. (1893b). Die Gattung Gastropodon. *Zoologische Jahrbücher, Abtheilung für Anatomie* 7: 281–308
- Bergh, R. (1897). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen von Dr C. Semper* 7(1): 1–51
- Bergh, R. (1898). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen von Dr C. Semper* 7(3): 117–158
- Bergh, R. (1900). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 7(4): 159–208
- Bergh, R. (1901). Bullacea. In Semper, C. *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 7: 209–312
- Bergh, R. (1902a). The Danish Expedition to Siam 1899–1900. I. Gastropoda Opisthobranchiata. *Det Kongelige Danske Videnskabernes Selskabs Skrifter* 6 Række, Naturvidenskabelig og matematisk Afdeling 12: 153–218
- Bergh, R. (1902b). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen von Dr C. Semper* 7(7): 313–382
- Bergh, R. (1905a). Die Opisthobranchiata der Siboga Expedition. *Siboga-Expeditie* 50: 1–248
- Bergh, R. (1905b). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 9(6): 57–115
- Bergh, R. (1908). Malacologische Untersuchungen. In Semper, C.G. (ed.) *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* 9(6): 119–178
- Bertsch, H. (1968). Effect of feeding by *Armina californica* on the bioluminescence of *Renilla koellikeri*. *The Veliger* 10: 440–441
- Bertsch, H. (1980a). The nudibranch *Aegires albopunctatus* (Polycerataceae: Aegiretidae) preys on *Leucilla nuttingi* (Porifera: Calcareae). *The Veliger* 22: 222–224
- Bertsch, H. (1980b). A new species of *Bornella* from tropical West-America (Mollusca: Opisthobranchia). *Spixiana* 3: 33–42
- Bertsch, H. & Johnson, S. (1981). *Hawaiian Nudibranchs: a guide for scuba divers, snorkelers, tide poolers and aquarists*. Oriental Publishing Company: Honolulu 112 pp.
- Betzer, P.R., Byrne, R.H., Acker, J.G., Lewis, C.S., Jolley, R.R. & Feely, R.A. (1984). The oceanic carbonate system: A reassessment of biogenic controls. *Science* 226: 1074–1077
- Bickell, L.R. & Chia, F.S. (1979). Organogenesis and histogenesis in the planktotrophic veliger of *Doridella steinbergae* (Opisthobranchia: Nudibranchia). *Marine Biology* 52: 291–313
- Bickell, L.R. & Kempf, S.C. (1983). Larval and metamorphic morphogenesis in the nudibranch *Melibe leonina* (Mollusca: Opisthobranchia). *Biological Bulletin, Marine Biological Laboratory Woods Hole* 165: 119–138
- Blainville, M.H. de. (1824). *Dictionnaire des Sciences Naturelles*. Vol. 32. Levrault: Paris & Strasbourg 567 pp.
- Blair, G.M. & Seapy, R.R. (1972). Selective predation and prey location in the sea slug *Navanax inermis*. *The Veliger* 15: 119–124
- Bleakney, J.S. (1988). The radula and penial style of *Alderia modesta* (Lovén, 1844). (Opisthobranchia: Ascoglossa) from populations in North America and Europe. *The Veliger* 31: 226–235
- Bleakney, J.S. (1989). Morphological variation in the radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) from Atlantic and Pacific populations. *The Veliger* 32: 171–181
- Bleakney, J.S. (1990). Indirect evidence of a morphological response in the radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) to different algal prey. *The Veliger* 33: 111–115
- Boas, J.E.V. (1886). *Spolia Atlantica*. Bidrag til Pteropodernes. Morphologi og Systematik am til Kundskaben om deres Geografiske Udbredelse. *Det Kongelige Danske Videnskabernes Selskabs Skifter*, 6. Række, Naturvidenskabelig og Mathematisk Afdeling 4: 1–248
- Boettger, C.R. (1963). Gastropoden mit zwei Schalenklappen. *Verhandlungen der Deutschen Zoologischen Gesellschaft in Wien* 1962: 403–439
- Bonnevie, K. (1933). Pteropoda from the "Michael Sars" North Atlantic Deep-sea Expedition. *Report on Science Research from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910*. Bergen III(1): 1–69
- Boss, K. (1982). Mollusca. Pp. 945–1166 in Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. Vol. 1. McGraw-Hill: New York
- Bouchet, P. (1975). Opisthobranches de profondeur de l'Océan Atlantique. 1. Cephalaspidae. *Cahiers de Biologie Marine* 16: 317–365
- Bouvier, E.L. (1893). Observations sur les Gastéropodes opisthobranches de la famille des Actaeonides (Campagne de l'Hirondelle, 3^e note. *Bulletin de la Société Philomathique de Paris* 5: 64–71
- Brace, R.C. (1977a). The functional anatomy of the mantle complex and columellar muscle of tectibranch molluscs (Gastropoda: Opisthobranchia), and its bearing on the evolution of opisthobranch organization. *Philosophical Transactions of the Royal Society of London, Series B* 277: 1–56
- Brace, R.C. (1977b). Anatomical changes in nervous and vascular systems during the transition from prosobranch to opisthobranch organization. *Transactions of the Zoological Society of London* 34: 1–25
- Brace, R.C. (1977c). Shell attachment and associated musculature in the Notaspidea and Anaspidea (Gastropoda: Opisthobranchia). *Transactions of the Zoological Society of London* 34: 27–43
- Brandley, B. (1984). Aspects of the ecology and physiology of *Elysia* cf. *furvacauda* (Mollusca: Sacoglossa). *Bulletin of Marine Science* 34: 207–219
- Bridges, C. (1975). Larval development of *Phyllaplysia taylori* Dall, with a discussion of development in the Anaspidea (Opisthobranchiata: Anaspidea). *Ophelia* 14: 161–184
- Brown, G.H. (1979). An investigation of the anatomy of *Colpodaspis pusilla* (Mollusca: Opisthobranchia) and a description of a new species of *Colpodaspis* from Tanzanian coastal waters. *Journal of Zoology, London* 187: 201–221
- Brown, G.H. & Picton, B.E. (1979). *Nudibranchs of the British Isles – a colour guide*. Underwater Conservation Society: Manchester 30 pp.

16. OPISTHOBRANCHIA

- Brown, H.H. (1934). A study of a tectibranch gastropod mollusc, *Philine aperta* (L.). *Transactions of the Royal Society of Edinburgh* 58: 179–210
- Brunckhorst, D.J. (1993). The systematics and phylogeny of phyllidiid nudibranchs (Doridoidea). *Records of the Australian Museum Supplement* 16 107 pp.
- Burn, R. (1957a). A new species of Opisthobranchia from Victoria (Mollusca: Gastropoda). *Victorian Naturalist* 74: 115–117
- Burn, R. (1957b). On some Opisthobranchia from Victoria. *Journal of the Malacological Society of Australia* 1(1): 11–29
- Burn, R. (1958). Further Victorian Opisthobranchia. *Journal of the Malacological Society of Australia* 1(2): 20–36
- Burn, R. (1959). Comments on the Australian umbraculacean Mollusca. *Journal of the Malacological Society of Australia* 1(3): 28–30
- Burn, R. (1960a). Australian bivalve gastropods. *Nature* 187: 44–46
- Burn, R. (1960b). On *Tylodina corticalis* (Tate), a rare opisthobranch from south-eastern Australia. *Journal of the Malacological Society of Australia* 1(4): 64–69
- Burn, R. (1960c). New names for two Victorian opisthobranch molluscs. *Journal of the Malacological Society of Australia* 1(4): 70
- Burn, R. (1961). Two new species and a new genus of opisthobranch molluscs from New South Wales. *Proceedings of the Royal Zoological Society of New South Wales* 1958–59: 131–135
- Burn, R. (1962a). On the new pleurobranch subfamily Berthellinae (Mollusca: Gastropoda); a revision and new classification of the species of New South Wales and Victoria. *Memoirs of the National Museum of Victoria* 25: 129–148
- Burn, R. (1962b). Descriptions of Victorian nudibranchiate Mollusca, with a comprehensive review of the Eolidacea. *Memoirs of the National Museum of Victoria* 25: 95–128
- Burn, R. (1963a). Australian Runcinacea (Mollusca: Gastropoda). *Australian Zoologist* 13: 9–22
- Burn, R. (1963b). Descriptions of Australian Eolidacea. (Mollusca: Opisthobranchia). 1. The genera *Catriona* and *Hervella*. *Journal of the Malacological Society of Australia* 1(7): 12–20
- Burn, R. (1964a). Australian sea slugs. *Australian Natural History* 14: 396–399
- Burn, R. (1964b). Descriptions of Australian Eolidacea (Mollusca: Opisthobranchia) 2. The genera *Nossis*, *Eubranchius*, *Trinchesia* and *Toorna*. *Journal of the Malacological Society of Australia* 1(8): 10–22
- Burn, R. (1965). Rediscovery and taxonomy of *Edentellina typica* Gatliff and Gabriel. *Nature* 206: 735–736
- Burn, R. (1966a). Some Opisthobranchs from southern Queensland. *Journal of the Malacological Society of Australia* 1(9): 96–110
- Burn, R. (1966b). The opisthobranchs of a Caulerpa microfauna from Fiji. *Proceedings of the Malacological Society of London* 37: 45–65
- Burn, R. (1966c). Descriptions of Australian Eolidacea (Mollusca: Opisthobranchia). 3. The genera *Tularia*, *Embletonia* and *Austraeolis*, with a note on *Tergipes pauculus* Burn, 1962. *Journal of the Malacological Society of Australia* 1(9): 25–35
- Burn, R. (1966d). Descriptions of Australian Eolidacea (Mollusca: Opisthobranchia). 4. The genera *Pleurolidia*, *Fiona*, *Learchis*, and *Cerberilla* from Lord Howe Island. *Journal of the Malacological Society of Australia* 10: 21–34
- Burn, R. (1967a). Descriptions of two new species of *Okenia* (Nudibranchia: Doridacea) from south-eastern Australia. *Proceedings of the Royal Zoological Society of New South Wales* 1965–66: 52–58
- Burn, R. (1967b). Notes on an overlooked nudibranch genus, *Roboastra* Bergh 1877, and two allied genera (Mollusca: Gastropoda). *Australian Zoologist* 14: 212–221
- Burn, R. (1967c). Revision of the genus *Hervella*. Opisthobranchia: Eolidacea. *Malacologia* 6: 223–230
- Burn, R. (1967d). First record of a pelagic eolid from Victoria. *Victorian Naturalist* 84: 116–117
- Burn, R. (1969). A memorial report on the Tom Crawford collection of Victorian Opisthobranchia. *Journal of the Malacological Society of Australia* 1(12): 64–106
- Burn, R. (1972). A guide to the Ascoglossa or sap-sucking sea-slugs of Australia. *Australian Natural History* 17: 174–178
- Burn, R. (1973a). Pearson Island Expedition 1969 –10. Opisthobranchs. *Transactions of the Royal Society of South Australia* 97: 201–205
- Burn, R. (1973b). Opisthobranch molluscs from the Australian sub-antarctic territories of Macquarie and Heard Islands. *Proceedings of the Royal Society of Victoria* 86: 39–46
- Burn, R. (1974a). Notes on some benthonic opisthobranchs from Port Phillip Bay, Victoria. *Journal of the Malacological Society of Australia* 3(1): 43–57
- Burn, R. (1974b). *Limapontia* in New Zealand waters. *Australian Shell News* No. 7: 5
- Burn, R. (1974c). The taxonomy and distribution of *Marianina rosea* (Pruvot-Fol, 1930) and *Thecacera pacifica* (Bergh, 1883) comb. nov. *The Veliger* 16: 305–306
- Burn, R. (1974d). *Limapontia* in Australia. *Australian Shell News* 7: 5
- Burn, R. (1975). Appendix: A list of dorid nudibranchs of Australia (Gastropoda: Opisthobranchia). Pp. 514–517 in Thompson, T.E. Dorid nudibranchs from eastern Australia (Gastropoda: Opisthobranchia). *Journal of Zoology, London* 176: 477–517
- Burn, R. (1977). Tropical opisthobranchs in South Australia. *Australian Shell News* No. 19: 8
- Burn, R. (1978). A review of Australian species of *Austrocylichna*, *Nipponatys*, *Cylichnatys* and *Diniatys* (Mollusca: Gastropoda: Haminoeidae). *Journal of the Malacological Society of Australia* 4: 93–112
- Burn, R. (1979). New locality records for *Lophopleurella wilsoni* (Opisthobranchia: Sacoglossa) (Tate, 1889) from southern Australia. *Journal of the Malacological Society of Australia* 4: 128
- Burn, R. (1980). The function of certain organs in the opisthobranch family Gastropteridae. *Journal of the Malacological Society of Australia* 4: 238
- Burn, R. (1984). Opisthobranchia. Pp. 67–74 in Phillips, D.A.B., Handreck, C., Bock, P.E., Burn, R., Smith, J.B. & Staples, D.A. (eds) *Coastal Invertebrates of Victoria: an atlas of selected species*. Marine Research group of Victoria/Museum of Victoria : Melbourne
- Burn, R. (1989). Opisthobranchs (Subclass Opisthobranchia). Pp. 725–788 in Shepherd, S.A. & Thomas, I.M. (eds) *Marine Invertebrates of Southern Australia. Part 2*. South Australian Government Printer : Adelaide
- Burn, R. (1990). An annotated list of opisthobranch molluscs from San Remo, Westernport, Victoria. *Marine News* (Newsletter of the Marine Research Group of Victoria) 100: 9–15
- Burn, R. & Bell, K.N. (1974a). Description of *Retusa chrysoma* Burn sp. nov. (Opisthobranchia) and its food resources from Corner Inlet, Victoria. *Memoirs of the National Museum of Victoria* 35: 115–119
- Burn, R. & Bell, K.N. (1974b). Description of *Retusa pelyx* Burn sp. nov. and its food resources from Swan Bay, Victoria. *Journal of the Malacological Society of Australia* 3: 37–42
- Burn, R. & Miller, M.C. (1969). A new genus, *Caldukia*, and an extended description of the type species, *Proctonotus ? affinis* Burn, 1958 (Mollusca: Gastropoda: Arminacea: Antiopellidae). *Journal of the Malacological Society of Australia* 1(12): 23–31
- Carefoot, T.H. (1967). Studies on a sublittoral population of *Aplysia punctata*. *Journal of the Marine Biological Association of the United Kingdom* 47: 335–350
- Carefoot, T.H. (1970). A comparison of absorption and utilisation of food energy in two species of tropical *Aplysia*. *Journal of Experimental Marine Biology and Ecology* 5: 47–62
- Carefoot, T.H. (1980). Studies on the nutrition and feeding preferences of *Aplysia*: development of an artificial diet. *Journal of Experimental Marine Biology and Ecology* 42: 241–252

- Carefoot, T.H. (1982). Nutrition of a coral rubble-inhabiting herbivore, the sea hare *Aplysia*. Pp. 665–669 in Gomez, D.G., Birkelang, C.E., Buddemeien, R.W., Johannes, R.E., Marsh, J.A. Jr, & Tsuda, R.T. (eds) *Proceedings of the Fourth International Coral Reef Congress, Manila 1981. Vol. 2*.
- Carefoot, T.H. (1985). Energy transformation by sea hares (*Aplysia*) in areas of coral rubble. Pp. 9–16 in Delesalle, B., Galzin, R. & Salvat, B. (eds) *Proceedings of the Fifth International Coral Reef Congress, Tahiti 1985. Vol. 4*
- Carefoot, T.H. (1987a). *Aplysia*: its biology and ecology. *Oceanography and Marine Biology, Annual Review* 25: 167–284
- Carefoot, T.H. (1987b). Diet and its effect on oxygen intake in the sea hare *Aplysia*. *Journal of Experimental Marine Biology and Ecology* 114: 275–287
- Carew, T.J., Hawkins, R.D. & Kandel, E.R. (1983). Differential classical conditioning of a defensive withdrawal reflex in *Aplysia californica*. *Science* 219: 397–400
- Carlson, C.H. & Hoff, P.J. (1971). Note on a bivalved gastropod from Guam. *Micronesica* 7: 237–238
- Carlson, C.H. & Hoff, P.J. (1973a). Two new species of Gastropodidae from Guam, Marianas Islands (Opisthobranchia: Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* 21: 141–151
- Carlson, C.H. & Hoff, P.J. (1973b). External description of a living *Aranucus bifidus* (Odhner, 1936). *The Veliger* 15: 172–173
- Carlson, C.H. & Hoff, P.J. (1974). The Gastropodidae of Guam, with descriptions of four new species (Opisthobranchia: Cephalaspidea). *Publications of the Seto Marine Biological Laboratory* 21: 345–364
- Carlson, C.H. & Hoff, P.J. (1978). The identifiable *Elysia* from Guam (Elysiidae, Sacoglossa, Opisthobranchia). *Micronesica* 14: 89–113
- Carlson, C.H. & Hoff, P.J. (1981). Preliminary check-list of the Opisthobranchia found on Guam. A working list of the marine organisms from Guam. *University of Guam Marine Laboratory Technical Report No. 70* pp. 46–53
- Cattaneo-Vietti, R. (1991). Nudibranch molluscs from the Ross Sea, Antarctica. *Journal of Molluscan Studies* Supplement, T.E. Thompson Memorial Issue 57(4): 223–228
- Challis, D.A. (1968). A new genus and species of the order Acochlidia (Mollusca: Opisthobranchia) from Melanesia. *Transactions of the Royal Society of New Zealand (Zoology)* 10: 191–197
- Challis, D.A. (1969a). *Philinoglossa marcusi* n.sp. (Mollusca: Opisthobranchia: Philinoglossacea) from the British Solomon Islands Protectorate. *Transactions of the Royal Society of New Zealand (Biological Sciences)* 11: 169–175
- Challis, D.A. (1969b). *Philine exigua* n.sp. (Opisthobranchia: Bullomorpha), a minute interstitial species from Melanesia. *Transactions of the Royal Society of New Zealand (Biological Sciences)* 11: 177–186
- Challis, D.A. (1969c). An ecological account of the marine interstitial opisthobranchs of the British Solomon Islands Protectorate. *Philosophical Transactions of the Royal Society of London, Series B* 255: 527–539
- Challis, D.A. (1969d). An interstitial fauna transect of a Solomon Islands sandy beach. *Philosophical Transactions of the Royal Society of London, Series B* 255: 517–526
- Challis, D.A. (1970). *Hedylopsis cornuta* and *Microhedyle verrucosa*, two new Acochlidia (Mollusca: Opisthobranchia) from the Solomon Islands Protectorate. *Transactions of the Royal Society of New Zealand (Biological Sciences)* 12: 29–40
- Chapman, D.J. & Fox, D.L. (1969). Bile pigment metabolism in the sea hare *Aplysia*. *Journal of Experimental Marine Biology and Ecology* 4: 71–78
- Chen, C. (1962). Ecological studies of the shell-bearing pteropods from the western part of the North Atlantic Ocean. PhD thesis, Boston University, Ann Arbor, Michigan 177 pp.
- Chen, C. (1964). Pteropod ooze from the Bermuda Pedestal. *Science* 144: 60–62
- Chen, C. & Bé, A.W.H. (1964). Seasonal distributions of euthecosomatous pteropods in the surface waters of five stations in the western North Atlantic. *Bulletin of Marine Science Gulf and Caribbean* 14: 185–220
- Chen, C. & Hillman, N.S. (1970). Shell-bearing pteropods as indicators of water masses off Cape Hatteras, North Carolina. *Bulletin of Marine Science of the Gulf and Caribbean* 20: 350–367 f050613
- Chia, F.-S. (1971). Oviposition, fecundity, and larval development of three sacoglossan opisthobranchs for the Northumberland coast, England. *The Veliger* 13: 319–325
- Chun, C. (1889). Bericht über eine nach den Canarischen Inseln im Winter 1887, 1888 ausgeführte Reise. 2. Abtheilung, Beobachtungen über die pelagische Tiefen- und Oberflächenfauna des östlichen Atlantischen Ozeans. *Mathematische und Naturwissenschaftliche Mittheilungen aus den Sitzungsberichten der Königlich Preussischen Akademie der Wissenschaften zu Berlin* Pt 6: 329–363 [519–553] Pl. 3
- Clark, K.B. (1982a). A new *Volvatella* (Mollusca: Ascoglossa) from Bermuda, with comments on the genus. *Bulletin of Marine Science* 32: 111–120
- Clark, K.B. (1982b). A new *Aplysiopsis* (Opisthobranchia: Hermaeidae) from central Florida, with a brief summary of the ceratiform families of the order Ascoglossa (= Sacoglossa). *Bulletin of Marine Science* 32: 213–219
- Clark, K.B. (1984). New records and synonymies of Bermuda opisthobranchs (Gastropoda). *The Nautilus* 98: 85–97
- Clark, K.B. & Busacca, M. (1978). Feeding specificity and chloroplast retention in four tropical Ascoglossa, with a discussion on the extent of chloroplast symbiosis and the evolution of the order. *Journal of Molluscan Studies* 44: 272–282
- Clark, K.B., Busacca, M. & Stirts, H. (1979). Nutritional aspects of the development of the ascoglossan, *Elysia cauzei*. Pp. 11–24 in Stancyk, S.E. (ed.) *Reproductive Ecology of Marine Invertebrates*. University of South Carolina Press : Columbia S.C.
- Clark, K.B. & Goetzfried, A. (1978). Zoogeographic influences on development patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies* 44: 283–294
- Clark, K.B. & Jensen, K. (1981). A comparison of egg-size, capsule size and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *International Journal of Invertebrate Reproduction* 3: 57–64
- Clark, K.B., Jensen, K.R. & Stirts, H.M. (1990). Survey of functional kleptoplasty among west Atlantic Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *The Veliger* 33: 339–345
- Clark, K.B., Jensen, K.R., Stirts, H.M. & Fermin, C. (1981). Chloroplast symbiosis in a non-elysiid mollusc, *Costasiella lilianae* Marcus (Hermaeidae: Ascoglossa (= Sacoglossa)): effects of temperature, light intensity and starvation on carbon fixing rate. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 160: 43–54
- Coleman, N. (1975). *What Shell is That?* Paul Hamlyn : Sydney 308 pp.
- Coleman, N. (1981). *A Field Guide to the Marine Life of South-Eastern Australia*. Rigby : Adelaide 167 pp.
- Coleman, N. (1989). *Nudibranchs of the South Pacific. Vol. 1. Sea Australia Resource Centre : Springwood, Queensland* 64 pp.
- Collingwood, C. (1881). On some new species of nudibranchiate mollusca from the eastern seas. *Transactions of the Linnean Society of London, Zoology* 2: 123–140
- Conover, R.J. & Lalli, C.M. (1972). Feeding and growth in *Clione limacina* (Phipps), a pteropod mollusc. *Journal of Experimental Marine Biology and Ecology* 9: 279–302
- Cossmann, M. (1897). The gastropods of the older Tertiary of Australia – Les Opisthobranches. *Transactions and Proceedings and Report of the Royal Society of South Australia* 21: 1–21
- Crane, S. (1971). The feeding and reproductive behaviour of the sacoglossan gastropod *Olea hansineensis* Agersborg, 1923. *The Veliger* 14: 57–59

- Croll, R.P. (1985). Sensory control of respiratory pumping in *Aplysia californica*. *Journal of Experimental Biology* 117: 15–27
- Curry, D. (1965). The English Palaeocene pteropods. *Proceedings of the Malacological Society of London* 36: 357–371
- Curry, D. & Rampal, J. (1979). Shell microstructure in fossil thecosome pteropods. *Malacologia* 18: 23–25 f050613
- Cuvier, G.L. (1797). Sur un nouveau genre de mollusque. *Bulletin des Sciences de la Société Philomathique de Paris* 1: 105
- Cuvier, G. (1804). Mémoire sur le genre *Doris*. *Annales du Muséum National d'Histoire Naturelle* 4: 447–473
- Cuvier, G. (1811). Mémoire sur les Acéres, ou Gastéropodes sans tentacules apparents. *Annales du Muséum National d'Histoire Naturelle* 16: 1–18
- Dakin, W.J. (1952). *Australian Seashores: a guide for the beach-lover, the naturalist, the shore fisherman, and the student*. Angus & Robertson: Sydney xii 372 pp.
- Dakin, W.J. & Colefax, A.N. (1936). *Ctilopsis*, a rare pelagic nudibranch of the family Phyllirhoidae (Bergh). *Proceedings of the Zoological Society of London* 1936: 455–460
- Dakin, W.J. & Colefax, A.N. (1940). The plankton of the Australian coastal waters off New South Wales. Part 1. *Publications of the University of Sydney, Zoology* 1: 1–215
- Davenport, J. & Beddington, A. (1990). Observations on the swimming and buoyancy of some thecosomatous pteropod gastropods. *Journal of Molluscan Studies* 56: 487–497
- De Freese, D.E. (1987). Burrowing activity and population biology of *Ascobulla ulla* Marcus (Opisthobranchia: Ascoglossa). *The Veliger* 30: 40–45
- Dell, R.K. (1956). The archibenthal Mollusca of New Zealand. *Dominion Museum Bulletin* 18: 1–235
- Dell, R.K. (1990). Antarctic Mollusca: with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand* 27: 1–311
- Diester-Haass, L. & van der Spoel, S. (1978). Late Pleistocene pteropod-rich sediment layer in the Northeast Atlantic and protoconch variation of *Clio pyramidata* Linné, 1767. *Palaeogeography, Palaeoclimatology and Palaeoecology* 24: 85–109
- Dimatteo, T. (1981). The inking behavior of *Aplysia dactylomela* (Gastropoda: Opisthobranchia). Evidence for distastefulness. *Marine Behaviour and Physiology* 7: 285–290
- Dimatteo, T. (1982). The ink of *Aplysia dactylomela* (Rang, 1828) (Gastropoda: Opisthobranchia) and its role as a defensive mechanism. *Journal of Experimental Marine Biology and Ecology* 57: 169–180
- Doty, M.S. & Aguilar-Santos, G. (1970). Transfer of toxic algal substances in marine food chains. *Pacific Science* 24: 351–355
- Dunbar, M.J. (1942). Marine macroplankton from the Canadian Eastern Arctic. II. Medusae, Siphonophora, Ctenophora, Pteropoda and Chaetognatha. *Canadian Journal of Resources* 20(D): 71–77
- Eales, N.B. (1921). *Aplysia*. Liverpool Marine Biological Committee Memoirs 24. *Proceedings and Transactions of the Liverpool Biological Society* 35: 183–266
- Eales, N.B. (1938). A systematic and anatomical account of the Opisthobranchia. *John Murray Expedition 1933–34, Scientific Reports* 5: 77–122
- Eales, N.B. (1960). Revision of the world species of *Aplysia* (Gastropoda: Opisthobranchia). *Bulletin of the British Museum (Natural History) (Zoology)* 5: 267–404
- Edlinger, K. (1982). Colour adaption in *Haminea navicula* (da Costa) (Mollusca – Opisthobranchia). *Malacologia* 22: 593–600
- Edmunds, M. (1963). *Berthelinia caribbea* n. sp., a bivalved gastropod from the west Atlantic. *Journal of the Linnean Society of London, Zoology* 44: 731–739
- Edmunds, M. (1966). Protective mechanisms in the Eolidacea (Mollusca, Nudibranchia). *Journal of the Linnean Society of London (Zoology)* 46: 27–71
- Edmunds, M. (1968a). Acid secretion in some members of Doridacea (Mollusca, Nudibranchia). *Proceedings of the Malacological Society of London* 38: 121–133
- Edmunds, M. (1968b). On the swimming and defensive response of *Hexabranchus marginatus* (Mollusca, Nudibranchia). *Journal of the Linnean Society of London (Zoology)* 47: 425–429
- Edmunds, M. (1971). Opisthobranchiate Mollusca from Tanzania (Suborder: Doridacea). *Zoological Journal of the Linnean Society* 50: 339–396
- Eliot, C.N.E. (1906a). Nudibranchs and tectibranchs from the Indo-Pacific. II. Notes on *Lophocercus*, *Lobiger*, *Haminea*, and *Newnesia*. *Journal of Conchology* 11: 298–315
- Eliot, C.N.E. (1906b). Nudibranchiata, with some remarks on the families and genera, and description of a new genus, *Doridomorpha*. In Gardiner, J.S. (ed.) *Fauna and Geography of the Maldives and Laccadive Archipelagoes* 2: 540–573
- Eliot, C.N.E. (1910). *A Monograph of the British Nudibranchiate Mollusca with Figures of the Species*. Part VIII (supplementary). Figures by the late Joshua Alder and the late Albany Hancock, and others. Ray Society: London 198 pp.
- Eliot, C.N.E. & Evans, T.J. (1908). *Doridoeides gardineri*: a doridiform cladohepatic nudibranch. *Quarterly Journal of Microscopical Science* 52: 279–299
- Essenberg, C. (1919). The pteropod *Desmopterus pacificus* sp. nov. *University of California Publications in Zoology* 19: 85–88
- Evans, T.J. (1950). A review of Peases genus *Volvatella*, together with a preliminary report on a new sacoglossan genus. *Proceedings of the Malacological Society of London* 28: 102–106
- Evans, T.J. (1953). The alimentary and vascular systems of *Alderia modesta* (Lovén) in relation to its ecology. *Proceedings of the Malacological Society of London* 29: 249–258
- Farfan, B.C. & Ramirez, L.F.B. (1988). Spawning and ontogeny of *Bulla gouldiana* (Gastropoda: Opisthobranchia: Cephalaspidea). *The Veliger* 31: 114–119
- Farmer, W.M. (1978). *Tambja* and *Roboastrea* (Mollusca: Opisthobranchia) from the Gulf of California and the Galapagos Islands. *The Veliger* 20: 375–385
- Farmer, W.M. (1980). *Sea-slug Gastropods*. W.M. Farmer Enterprises Inc.: Tempe, Arizona 117 pp.
- Ferry, G. (1986). Memory, molluscs and molecules. *New Scientist* 109: 52–55
- Fiege, D. (1990). Morphology of the wings of euthecosomatous pteropods. *American Malacological Bulletin* 8: 27–36
- Foale, S.J. & Willan, R.C. (1987). Scanning and transmission electron microscope study of specialized mantle structures in dorid nudibranchs (Gastropoda: Opisthobranchia: Anthobranchia). *Marine Biology* 95: 547–557
- Forbes, E. & Hanley, S. (1848–1853). *A History of British Mollusca, and Their Shells*. Van Voorst: London 4 vols, 477 pp., 557 pp., 616 pp., 300 pp.
- Franc, A. (1968). Sous-classe des Opisthobranches. Pp. 608–893 in Grassé, P. (ed.) *Traité de Zoologie*. Vol. 5. Pt 3. Masson & Co. Paris
- Francis, M.P. (1980). Habitat, food and reproductive activity of the nudibranch *Hexabranchus sanguineus* on Tongatapu Island. *The Veliger* 22: 252–258
- Fretter, V. (1939). The structure and function of the alimentary canal of some tectibranch molluscs, with a note on excretion. *Transactions of the Royal Society of Edinburgh* 59: 599–646
- Fretter, V. (1960). Observations on the tectibranch *Ringicula buccinea* (Brocchi). *Proceedings of the Zoological Society of London* 135: 537–549
- Fretter, V. & Graham, A. (1954). Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *Journal of the Marine Biological Association of the United Kingdom* 33: 565–585
- Fretter, V. & Graham, A. (1962) *British Prosobranch Molluscs. Their functional anatomy and ecology*. Ray Society: London xvi 755 pp.
- Fretter, V. & Ko, B.H. (1979). The specialization of the aplysiid gut. *Malacologia* 18: 7–11
- Fretter, V. & Ko, B.H. (1984). Observations of the reproductive system of the aplysiid *Dolabella auricularia*. *Malacologia* 25: 193–201

- Furnestin, M.-L. (1979). Planktonic molluscs as hydrological and ecological indicators. Pp. 175–194 in van der Spoel, S., van Bruggen, A.C. & Lever, J. (eds) *Pathways in Malacology*. Bohn, Scheltema & Holkema: Utrecht
- Gantes, H. & Cornet, M. (1981). Précisions nouvelles sur l'anatomie de *Roxania utriculus* (Brocchi, 1814) (Mollusque, Gastéropode, Opisthobranchie). *Bulletin de Société Zoologique de France* 106: 183–186
- García, F.J. & García-Gómez, J.C. (1990). Anatomy of the circulatory system of the nudibranch *Platydoris argo* (Linne, 1767) with comparisons among Doridacea (Gastropoda: Opisthobranchia). *The Veliger* 33: 166–173
- Gascoigne, T. (1956). Feeding and reproduction in the Limapontiidae. *Transactions of the Royal Society of Edinburgh* 63: 129–151
- Gascoigne, T. (1974a). A note of some sacoglossan penial styles (Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society* 55: 53–59
- Gascoigne, T. (1974b). A re-examination of the central nervous system of *Alderia modesta* (Lovén). *Transactions of the Royal Society of Edinburgh* 69: 137–146
- Gascoigne, T. (1975). The radula and reproductive system of *Olea hansineensis* Agersborg, 1923 (Gastropoda; Opisthobranchia; Sacoglossa). *The Veliger* 17: 313–317
- Gascoigne, T. (1976). The reproductive systems and classification of the Stiligeridae (Opisthobranchia: Sacoglossa). *Journal of the Malacological Society of Australia* 3: 157–172
- Gascoigne, T. (1978). The internal anatomy of *Stiliger fuscatus* (A. Gould, 1870) (Opisthobranchia: Sacoglossa). *Zoological Journal of the Linnean Society of London* 63: 265–274
- Gascoigne, T. (1979a). A redescription of *Caliphylla mediterranea* Costa, 1867 (Opisthobranchia: Ascoglossa). *Journal of Molluscan Studies* 45: 300–311
- Gascoigne, T. (1979b). Observations on the anatomy of *Hermaea variopicta* (Opisthobranchia: Ascoglossa). *Journal of Zoology, London* 187: 223–233
- Gascoigne, T. (1985). A provisional classification of families of the order Ascoglossa (Gastropoda: Nudibranchiata). *Journal of Molluscan Studies* 51: 8–22
- Gascoigne, T. & Sartory, P.K. (1974). The teeth of three bivalve gastropods and three other species of the order Sacoglossa. *Proceedings of the Malacological Society of London* 41: 109–124
- Gascoigne, T. & Sordi, M. (1980). A redescription of *Placida viridis* Trinchese, 1873 (Gastropoda: Ascoglossa). *Journal of Conchology* 30: 167–179
- Ghiselin, M.T. (1963). On the functional and comparative anatomy of *Runcina seteosis* Baba, an opisthobranch gastropod. *Publications of the Seto Marine Biological Laboratory* 11: 389–398
- Ghiselin, M.T. (1966). Reproductive function and the phylogeny of opisthobranch gastropods. *Malacologia* (for 1965) 3: 327–378
- Ghiselin, M.T., Degbens, E.T., Spencer, D.W. & Parker, R.H. (1967). A phylogenetic survey of molluscan shell matrix proteins. *Breviora* 262: 1–35
- Gibson, G.D. & Chia, F.-S. (1989). Embryology and larval development of *Haminoea vesicula* Gould (Opisthobranchia: Cephalaspidea). *The Veliger* 32: 409–411
- Gibson, G.D., Toews, D.P. & Bleakney, J.S. (1986). Oxygen production and consumption in the sacoglossan (= ascoglossan) *Elysia chlorotica* Gould. *The Veliger* 28: 397–400
- Gillett, K. & Yaldwyn, J.C. (1969). *Australian Seashores in Colour*. A.H. & A.W. Reed: Sydney 112 pp.
- Gilmer, R.W. (1972). Free-floating mucus webs: a novel feeding adaptation for the open ocean. *Science* 176: 1239–1240
- Gilmer, R.W. (1974). Some aspects of feeding in thecosomatous pteropod molluscs. *Journal of Experimental Marine Biology and Ecology* 15: 127–144
- Gilmer, R.W. & Harbison, G.R. (1986). Morphology and field behavior of pteropod molluscs: feeding methods in the families Cavoliniidae, Limaciniidae and Peraclididae (Gastropoda: Thecosomata). *Marine Biology* 91: 47–57
- Gilmer, R.W. & Lalli, C.M. (1990). Bipolar variation in *Clione*, a gymnosomatous pteropod. *American Malacological Bulletin* 8: 67–75
- Gohar, H.A.F. & Abul-Ela, I.A. (1957). The development of *Berthellina citrina* (Mollusca, Opisthobranchiata). *Publications of the Marine Biological Station, al-Ghardaqa, Red Sea* 9: 69–83
- Gohar, H.A.F. & Soliman, G.N. (1963). The biology and development of *Hexabanchus sanguineus* (Rüpp. & Leuck.) (Gastropoda, Nudibranchiata). *Publications of the Marine Biological Station, al-Ghardaqa, Red Sea* 12: 219–247
- Gonor, J.J. (1961a). Observations on the biology of *Lobiger serradifalci*, a shelled sacoglossan opisthobranch from the Mediterranean. *Vie et Milieu* 12: 381–403
- Gonor, J.J. (1961b). Observations on the biology of *Hermaea smithi*, a sacoglossan opisthobranch from the west coast of North America. *The Veliger* 4: 85–98
- Gosliner, T.M. (1979). A review of the systematics of *Cylichnella* Gabb (Opisthobranchia: Scaphandridae). *The Nautilus* 93: 85–92
- Gosliner, T.M. (1980). Systematics and phylogeny of the Aglajidae (Opisthobranchia: Mollusca). *Zoological Journal of the Linnean Society* 68: 325–360
- Gosliner, T.M. (1981a). Origins and relationships of primitive members of the Opisthobranchia (Mollusca: Gastropoda). *Biological Journal of the Linnean Society* 16: 197–225
- Gosliner, T.M. (1981b). The South African Janolidae (Mollusca, Nudibranchia) with the description of a new genus and two new species. *Annals of the South African Museum* 86: 1–42
- Gosliner, T.M. (1984). Two new species of *Gastropodon* (Gastropoda: Opisthobranchia) from southern Africa. *Publications of the Seto Marine Biological Laboratory* 29(4-6): 231–247
- Gosliner, T.M. (1987a). *Nudibranchs of Southern Africa. A Guide to Opisthobranch Molluscs of Southern Africa*. Sea Challengers & J. Hamann in association with the California Academy of Sciences: Monterey, California 136 pp.
- Gosliner, T.M. (1987b). Review of the Nudibranch genus *Melibe* (Opisthobranchia: Dendronotacea) with descriptions of two new species. *The Veliger* 29: 400–414
- Gosliner, T.M. (1988). The Philinacea (Mollusca: Gastropoda: Opisthobranchia) of Aldabra Atoll, with descriptions of five new species and a new genus. *Bulletin of the Biological Society of Washington* 8: 79–100
- Gosliner, T.M. (1989). Revision of the Gastropodidae (Opisthobranchia: Cephalaspidea) with descriptions of a new genus and six new species. *The Veliger* 32: 333–381
- Gosliner, T.M. (1991). Four new species and a new genus of opisthobranch gastropods from the Pacific Coast of North America. *The Veliger* 34: 272–290
- Gosliner, T.M. & Armes, P.T. (1984). A new species of *Gastropodon* from Florida (Gastropoda: Opisthobranchia). *The Veliger* 27: 54–64
- Gosliner, T.M. & Bertsch, H. (1985). Records and morphology of *Lomanotus stauberi* Clark & Goetzfried, 1976, from the Panamic Pacific. *The Veliger* 27: 397–405
- Gosliner, T.M. & Bertsch, H. (1988). A review of the genus *Berthella* (Opisthobranchia: Notaspidea) from the Pacific coast of North America. *The Veliger* 31: 46–67
- Gosliner, T.M. & Ghiselin, M.T. (1984). Parallel evolution in opisthobranch gastropods and its implications for phylogenetic methodology. *Systematic Zoology* 33: 255–274
- Gosliner, T.M. & Griffiths, R.J. (1981). Description and revision of some South African aeolidacean Nudibranchia (Mollusca, Gastropoda). *Annals of the South African Museum* 84: 105–150
- Gosliner, T.M. & Willan, R.C. (1991). Review of the Flabellinidae (Nudibranchia: Aeolidacea) from the tropical Indo-Pacific, with the descriptions of five new species. *The Veliger* 34: 97–133
- Gould, A.A. (1852). Mollusca and shells. *United States Exploring Expedition: during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. Vol. 12*. C. Sherman: Philadelphia 16 pp., atlas 52 leaves

- Grahame, J. (1969). The biology of *Bethelinia caribbea* Edmunds. *Bulletin of Marine Science* 19: 868–879
- Gray, J.E. (1850). Preface in Gray, M.E. *Figures of Molluscan Animals, selected from various authors*. Vol. 3. Longmans, Brown, Green & Longmans: London
- Griffiths, R.J. (1985). Description of a new South African arminacean and the proposed re-instatement of the genus *Athila* Bergh (Mollusca, Opisthobranchia). *Annals of the South African Museum* 95: 269–280
- Guiart, J. (1901). Contribution à l'étude des Gastéropodes Opisthobranches et en particulier des Céphalaspides. *Mémoires de la Société de Zoologie de France* 14: 5–219
- Gunthorpe, L. & Cameron, A.M. (1987). Bioactive properties of extracts from Australian dorid nudibranchs. *Marine Biology* 94: 39–43
- Habe, T. (1950a). Ringiculidae and Retusidae in Japan. *Illustrated Catalogue of Japanese Shells* 1(2): 7–16
- Habe, T. (1950b). Hydatinidae, Bullidae and Akeridae in Japan. *Illustrated Catalogue of Japanese Shells* 1(3): 17–24
- Habe, T. (1950c). Pupidae in Japan. *Illustrated Catalogue of Japanese Shells* 1(6): 39–44
- Habe, T. (1952). Atyidae in Japan. *Illustrated Catalogue of Japanese Shells* 1(20): 137–152
- Habe, T. (1964). *Shells of the Western Pacific in Color*. Vol. 2. Hoikusha Publishing: Osaka 233 pp. 66 pls
- Hadfield, M.G. & Switzer-Dunlap, M. (1984). Opisthobranchs. Pp. 209–350 in Wilbur, K.M. (ed.) *The Mollusca*. Vol. 7. *Reproduction*. Academic Press: London
- Haefelfinger, H.R. (1962). Quelques faits concernant la nutrition chez *Favorinus branchialis* (Rathke 1806) et *Stiliger vesiculosus* (Deshayes 1864), deux mollusques opisthobranches. *Revue Suisse de Zoologie* 69: 311–316
- Hain, S. Wägele, H. & Willan, R.C. (1993). *Tomthompsonia spiroconchialis* Wägele & Hain, 1991 (Opisthobranchia: Pleurobranchidae): a junior synonym of *Adeorbis antarcticus* Thiele, 1912 (Prosobranchia: Truncatelloidea) with notes on diet and histology. *Journal of Molluscan Studies* 59: 366–370
- Halstead, B.W. (1965). *Poisonous and Venomous Marine Animals of the World*. Vol. 1. *Invertebrates*. United States Government Printing Office: Washington, D.C. xxxv 994 pp.
- Hamada, S. & Ino, T. (1957). Ecological studies on a predator for commercial clams, *Philine japonica* Lischke. *Bulletin of the Tokai Regional Fisheries Research Laboratory* 16: 41–48
- Hamatani, I. (1960). Notes on veligers of Japanese opisthobranchs (1). *Publications of the Seto Marine Biological Laboratory* 8: 59–69
- Hamatani, I. (1961). Notes on veligers of Japanese opisthobranchs (3). *Publications of the Seto Marine Biological Laboratory* 9: 67–79
- Hamatani, I. (1967). Notes on veligers of Japanese opisthobranchs (7). *Publications of the Seto Marine Biological Laboratory* 15: 121–131
- Hamatani, I. (1972). A new species of *Volvatella* Pease, 1860, found in the "Caulerpa microfauna" in the province of Kii, Middle Japan (Opisthobranchia: Sacoglossa). *Publications of the Seto Marine Biological Laboratory* 21: 13–20
- Hamatani, I. (1976). Preliminary accounts of a new species of *Volvatella* Pease, 1860, *V. viridis* sp. nov., found in the caulerpa microfauna in Japan (Opisthobranchia: Sacoglossa). *Publications of the Seto Marine Biological Laboratory* 22: 371–376
- Hamatani, I. (1991). *Sohgenia palauensis* n. gen. & sp., a new ascoglossan opisthobranch from the Palau Islands collected by the R/V Sohgen-Maru. *Venus* 50: 85–91
- Hamilton, P.V. & Ambrose, H.W. II (1975). Swimming and orientation in *Aplysia brasiliana* (Mollusca: Gastropoda). *Marine Behaviour and Physiology* 3: 131–143
- Harry, H.W. (1967). A review of the living tectibranch snails of the genus *Volvulella*, with descriptions of a new subgenus and species from Texas. *The Veliger* 10: 133–147
- Hartley, T.W. (1964). Egg laying and early development of *Umbraculum sinicum* Gmelin. *Journal of the Malacological Society of Australia* 1(8): 33–35
- Hasselt, J.C. van (1824). Uittreksel uit eenen Brief van Dr J.C. Hasselt, aan Prof. van Swinderen. *Algemeene Konsten Letterbode* 1824 No. 3: 34–39
- Haszprunar, G. (1985a). The fine morphology of the osphradial sense organs of the Mollusca. I. Gastropoda, Prosobranchia. *Philosophical Transactions of the Royal Society of London, Series B* 307: 457–496
- Haszprunar, G. (1985b). The fine morphology of the osphradial sense organs of the Mollusca. II. Allogastropoda (Architectonicidae, Pyramidellidae). *Philosophical Transactions of the Royal Society of London, Series B* 307: 497–505
- Haszprunar, G. (1988). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies* 54: 367–441
- Haszprunar, G. & Huber, G. (1990). On the central nervous system of Smeagolidae and Rhodopidae, two families questionably allied with the Gymnomorpha (Gastropoda: Euthyneura). *Journal of Zoology, London* 220: 185–199
- Haynes, A. & Kenchington, W. (1991). *Acochlidium fijiensis* sp. nov. (Gastropoda: Opisthobranchia: Acochlididae) from Fiji. *The Veliger* 34: 166–171
- Healy, J.M. (1993). Comparative sperm ultrastructure and spermiogenesis in basal heterobranch gastropods (Valvatoidea, Architectonicoidea, Rissoelloidea, Omalogyroidea, Pyramidelloidea) (Mollusca). *Zoologica Scripta* 22: 263–276
- Healy, J.M. & Willan, R.C. (1984). Ultrastructure and phylogenetic significance of notaspidean spermatozoa (Mollusca: Gastropoda: Opisthobranchia). *Zoologica Scripta* 13: 107–120
- Healy, J.M. & Willan, R.C. (1991a). Nudibranch spermatozoa: comparative ultrastructure and systematic importance. *The Veliger* 34: 134–165
- Healy, J.M. & Willan, R.C. (1991b). Sperm ultrastructure of the tropical notaspidean *Pleurehdera haraldi* with evaluation of the phylogenetic position of the genus. *Journal of Molluscan Studies Supplement*, T.E. Thompson Memorial Issue 57(4): 113–118
- Hedley, C. (1902). Studies on Australian Mollusca. Part V. *Proceedings of the Linnean Society of New South Wales* 26: 700–708
- Hedley, C. (1903). Mollusca. Part 2. Scaphopoda and Gastropoda. *Scientific results of the trawling expedition of H.M.C.S. Thetis*, off the coast of New South Wales, in February and March, 1898. *Australian Museum Memoir* 4: 327–402
- Hedley, C. (1907). The results of deepsea investigation in the Tasman Sea. II. The expedition of the "Woy Woy". 2. Mollusca from eight hundred fathoms, thirty-five miles east of Sydney. *Records of the Australian Museum* 6: 356–364
- Hedley, C. (1910a). The marine fauna of Queensland. *Reports of the Australasian Association for the Advancement of Science* 12: 329–371
- Hedley, C. (1910b). Addendum to catalogue of marine mollusca of Queensland. *Reports of the Australasian Association for the Advancement of Science* 12: 809–810
- Hedley, C. (1912). Descriptions of some new or noteworthy shells in the Australian Museum. *Records of the Australian Museum* 8: 131–160
- Hedley, C. (1920). Concerning *Edenttellina*. *Proceedings of the Malacological Society of London* 14: 74–76
- Hoegh-Guldberg, I.O. & Hinde, R. (1986). Studies on a nudibranch that contains zooxanthellae. I. Photosynthesis, respiration and the translocation of newly fixed carbon by zooxanthellae in *Pteraeolidia ianthina*. *Proceedings of the Royal Society of London, Series B* 228: 493–509
- Hoegh-Guldberg, I.O., Hinde, R. & Muscatine, L. (1986). Studies on a nudibranch that contains zooxanthellae. II. Contribution of zooxanthellae to animal respiration (CZAR) in *Pteraeolidia ianthina* with high and low densities of zooxanthellae. *Proceedings of the Royal Society of London, Series B* 228: 511–521
- Hoff, P.J. & Carlson, C.H. (1990). A new Runcinacea from the Mariana Islands (Gastropoda: Opisthobranchia). *Venus* 49: 263–269

- Hoffman, H. (1940). Opisthobranchia. Pp. 1–90 in Bronns, H.G. Klassen und Ordnungen des Tierreichs. 3. Band: Mollusca, II. Abteilung: Gastropoda, 3. Buch: Opisthobranchia, Teil 2, 1. Lieferung
- Høisæter, T. (1986). An annotated check-list of marine molluscs from the Norwegian coast and adjacent waters. *Sarsia* 71: 73–145
- Holleman, J.J. (1972). Observations on growth, feeding and reproduction, and development in the opisthobranch, *Fiona pinnata* (Eschscholtz). *The Veliger* 15: 142–146
- Horikoshi, M. (1967). Reproduction, larval features and life history of *Philine denticulata* (J. Adams) (Mollusca – Tectibranchia). *Ophelia* 4: 43–84
- Howells, H.H. (1936). The anatomy and histology of the gut of *Cymbulia peronii* (Blainville). *Proceedings of the Malacological Society of London* 22: 62–72
- Hsiao, S.C.T. (1939a). The reproductive system and spermatogenesis of *Limacina (Spiratella) retroversa* (Flem.). *Biological Bulletin, Marine Biological Laboratory Woods Hole* 76: 7–25
- Hsiao, S.C.T. (1939b). The reproduction of *Limacina retroversa* (Flem.). *Biological Bulletin, Marine Biological Laboratory Woods Hole* 76: 280–303
- Hurst, A. (1965). Studies on the structure and function of the feeding apparatus of *Philine aperta* with a comparative consideration of some other opisthobranchs. *Malacologia* 2: 281–347
- Hurst, A. (1967). The egg masses and veligers of thirty northeast Pacific opisthobranchs. *The Veliger* 9: 255–288
- Hurst, A. (1968). The feeding mechanism and behaviour of the opisthobranch *Melibe leonina*. *Symposia of the Zoological Society of London* No. 22: 151–166
- Huxley, T.H. (1853). On the morphology of the cephalous Mollusca, as illustrated by the anatomy of certain Heteropoda and Pteropoda collected during the voyage of the H.M.S. *Rattlesnake* in 1846–50. *Philosophical Transactions of the Royal Society, London* 143: 29–65
- Hyman, L.H. (1967). *The Invertebrates. Vol. 6 Mollusca 1*. McGraw-Hill: New York vii 792 pp.
- Ihering, H. von (1892). Zur Kenntniss der Sacoglossen. *Nova Acta der Ksl. Leopoldino-Carolinae Deutschen Akademie der Naturforscher* 58: 361–435
- ICZN (1981). Opinion 1182. Tethyidae in Mollusca, Porifera and Tunicata: removal of the homonymy. *Bulletin of Zoological Nomenclature* 38: 174–177
- Iredale, T. (1925). Mollusca from the continental shelf of eastern Australia. *Records of the Australian Museum* 14: 243–270
- Iredale, T. (1929). Strange molluscs in Sydney Harbour. *Australian Zoologist* 5: 337–352
- Iredale, T. (1936). Australian molluscan notes. No. 2. *Records of the Australian Museum* 19: 267–340
- Janssen, A.W. (1989). Pteropoda (Gastropoda, Euthecosomata) from the Australian Cainozoic. *Scripta Geologica* 91: 1–76
- Janssen, A.W. (1990). Long distance correlation of Cainozoic deposits by means of planktonic gastropods ("pteropods"); some examples of future possibilities. *Tertiary Research* 11: 65–72
- Janssen, R. (1979). *Berthelinia* und *Julia* aus dem Oligozan von SW-Frankreich (Gastropoda: Sacoglossa). *Archiv für Molluskenkunde* 110: 75–79
- Jensen, K.R. (1975a). The importance of *Limapontia capitata* (Mueller) (Opisthobranchia, Sacoglossa) as a primary consumer in the *Cladophora*-belt. *Tenth European Symposium on Marine Biology, Ostend, Belgium, September 17–23, 1975* 2: 339–350
- Jensen, K.R. (1975b). Food preference and food consumption in relation to growth of *Limapontia capitata* (Opisthobranchia, Sacoglossa). *Ophelia* 14: 1–14
- Jensen, K.R. (1977). Optimal salinity and temperature intervals of *Limapontia capitata* (Opisthobranchia, Sacoglossa) determined by growth and heart rate measurements. *Ophelia* 16: 175–185
- Jensen, K.R. (1980). A review of sacoglossan diets, with comparative notes on radular and buccal anatomy. *Malacological Review* 13: 55–77
- Jensen, K.R. (1981a). Influence of filament diameter on food preference and growth in *Oxynoe azuropunctata* Jensen, 1980 and *Elysia cauze* Marcus, 1957 (Opisthobranchia: Ascoglossa). *Ophelia* 20: 127–135
- Jensen, K.R. (1981b). Observations on feeding methods in some Florida ascoglossans. *Journal of Molluscan Studies* 47: 190–197
- Jensen, K.R. (1984). Defensive behaviour and toxicity of ascoglossan opisthobranch *Mourgona germainae* Marcus. *Journal of Chemical Ecology* 10: 475–486
- Jensen, K.R. (1985). Annotated checklist of Hong Kong Ascoglossa (Mollusca: Opisthobranchia), with descriptions of four new species. Pp. 77–107 in Morton, J.E. & Dudgeon, D. (eds) *The malacofauna of Hong Kong and southern China. 2. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong 6–24 April 1983*. Hong Kong University Press: Hong Kong
- Jensen, K.R. (1986). Observations on copulation in two species of *Elysia* from Florida (Opisthobranchia: Ascoglossa). *Ophelia* 25: 25–32
- Jensen, K.R. (1989). A new species of *Cylindrobulla* from Phuket, Thailand, with a discussion on the systematic affiliation of the genus. *Phuket Marine Biological Center, Research Bulletin* 52: 1–11
- Jensen, K.R. (1990a). Three new species of Ascoglossa (Mollusca, Opisthobranchia) from Hong Kong, and a description of the internal anatomy of *Costasiella pallida* Jensen, 1985. Pp. 419–432 in Morton, B. (ed.) *Proceedings of the 2nd International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986. Vol. 1. Introduction and taxonomy*. Hong Kong University Press: Hong Kong
- Jensen, K.R. (1990b). Feeding behaviour of some Hong Kong Ascoglossa (Mollusca: Opisthobranchia). Pp. 961–978 in Morton, B. (ed.) *Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986. Vol. 3. Behaviour, morphology, physiology and pollution*. Hong Kong University Press: Hong Kong
- Jensen, K.R. (1990c). *Splanchnotrophus elysiae* n. sp. (Copepoda, Splanchnotrophidae) found parasitizing in the sacoglossan opisthobranch *Elysia australis* (Quoy & Gaimard, 1832). Pp. 291–296 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia. Vol. 1. Western Australian Museum: Perth*
- Jensen, K.R. (1990d). Foraging behaviour of two Australian species of *Elysia* (Mollusca, Opisthobranchia). Pp. 541–551 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia. Vol. 2. Western Australian Museum: Perth*
- Jensen, K.R. (1991). Comparison of alimentary systems in shelled and non-shelled Sacoglossa (Mollusca, Opisthobranchia). *Acta Zoologica* 72: 143–150
- Jensen, K.R. (1992). Anatomy of some Indo-Pacific Elysiidae (Opisthobranchia: Sacoglossa (= Ascoglossa)), with a discussion of the generic division and phylogeny. *Journal of Molluscan Studies* 58: 257–296
- Jensen, K.R. (1993a). Sacoglossa (Mollusca, Opisthobranchia) from Rottnest Island and central Western Australia. Pp. 207–253 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia, Rottnest Island, January 1991. Vol. 1. Western Australian Museum: Perth*
- Jensen, K.R. (1993b). Sacoglossa (Mollusca: Opisthobranchia) – specialist herbivores and partial predators: integrating ecological, physiological and morphological data. Pp. 437–458 in Morton, B.S. & Tseng, C.K. (eds) *The Marine Biology of the South China Sea. Proceedings of the 1st International Conference on the Marine Flora and Fauna of Hong Kong and the South China Sea*. Hong Kong University Press: Hong Kong

- Jensen, K.R. (1993c). Evolution of buccal apparatus and diet radiation in the Sacoglossa (Opisthobranchia). *Bolletino Malacologico* 29: 147–172
- Jensen, K.R. (1993d). Morphological adaptations and plasticity of radular teeth of the Sacoglossa (=Ascoglossa) (Mollusca: Opisthobranchia) in relation to their food plants. *Biological Journal of the Linnean Society* 48: 135–155
- Jensen, K.R. (in press). Sacoglossa (Mollusca, Opisthobranchia) from Darwin Harbour. In Megirian, D. (ed.) *Proceedings of the 6th International Marine Biological Workshop: The Marine Flora and Fauna of Darwin Harbour, Northern Territory, Australia* Northern Territory Museum of Arts and Sciences : Darwin
- Jensen, K.R. & Clark, K.B. (1983). Annotated checklist of Florida ascoglossan Opisthobranchia. *The Nautilus* 97: 1–13
- Jensen, K.R. & Wells, F.E. (1990). Sacoglossa (= Ascoglossa) (Mollusca, Opisthobranchia) from southern Western Australia. Pp. 297–331 in Wells, F.E., Walker, D.I., Kirkman, H. & Lethbridge, R. (eds) *Proceedings of the Third International Marine Biological Workshop. The marine Flora and Fauna of Albany, Western Australia. Vol. 1. Western Australian Museum : Perth*
- Johansson, J. (1954). On the pallial gonoduct of *Actaeon tornatilis* (L.) and its significance for the phylogeny of the Euthyneura. *Zoologiska Bidrag från Uppsala* 30: 223–232
- Johnson, S. (1984). A new Indo-West Pacific species of the dendronotacean nudibranch *Bornella* (Mollusca: Opisthobranchia) with anguilliform swimming behaviour. *Micronesica* 19: 17–26
- Johnson, S. & Boucher, L.M. (1983). Notes on some Opisthobranchia (Mollusca: Gastropoda) from the Marshall Islands, including 57 new records. *Pacific Science* 37: 251–291
- Jonas, M. (1984). Anatomie, Histologie, und Feinstruktur der Doridier-Kieme (Gastropoda, Nudibranchia). Thesis, University of Münster. (Not seen).
- Jonas, M. (1986). Ultrastructure of the gill epithelia of the dorid nudibranchs *Archidoris pseudoargus* and *Peltodoris atromaculata* Bergh, 1880 (Gastropoda: Opisthobranchia). *The Veliger* 29: 207–216
- Just, J. (1977). A new genus and species of corophiid Amphipoda from pteropod shells of the bathyal western Atlantic, with notes on related genera (Crustacea). *Steenstrupia* 4: 131–138
- Kandel, E.R. (1979). *Behavioral Biology of Aplysia: A Contribution to the Comparative Study of Opisthobranch Molluscs*. W.H. Freeman & Company : San Francisco 463 pp.
- Kawaguti, S. (1968). Electron microscopy of sheathed muscle fibres of an opisthobranch mollusk. *Biological Journal of Okayama University* 14: 13–20
- Kawaguti, S. (1981). A new bivalved gastropod, *Julia zebra* n. sp. *Bulletin of Kawasaki Paramedical College* 1: 9–13
- Kawaguti, S. & Baba, K. (1959). A preliminary note on a two-valved sacoglossan gastropod, *Tamanovalva limax*, n. gen., n. sp., from Tamano, Japan. *Biological Journal of Okayama University* 5: 177–184
- Kawaguti, S. & Kamishima, Y. (1964). Electron microscope study of the iridophores of opisthobranchiate mollusks. *Biological Journal of Okayama University* 10: 83–91
- Kawaguti, S., Kamishima, Y. & Nakamura, A. (1966). Electron microscopy on the pigment and mucous cells in an opisthobranchiate mollusk. *Biological Journal of Okayama University* 12: 23–34
- Kawaguti, S. & Yamasu, T. (1960). Spawning habits of a bivalved gastropod, *Tamanovalva limax*. *Biological Journal of Okayama University* 6: 133–149
- Kawaguti, S. & Yamasu, T. (1965). Electron microscopy on the symbiosis between an elysiid gastropod and chloroplasts of a green alga. *Biological Journal of Okayama University* 11: 57–65
- Kawaguti, S. & Yamasu, T. (1966). Feeding and spawning habits of a bivalved gastropod, *Julia japonica*. *Biological Journal of Okayama University* 12: 1–9
- Kawaguti, S. & Yamasu, T. (1982). A new bivalved gastropod, *Julia mishimaensis* n. sp. *Proceedings of the Japan Academy, Series B, Physical and Biological Sciences* 58: 29–31
- Kawaguti, S., Yamamoto, M. & Kamishima, Y. (1965). Electron microscopy on the symbiosis between blue-green algae and an opisthobranch, *Placobranchus*. *Proceedings of the Japan Academy* 41: 614–617
- Kay, E.A. (1961). A new opisthobranch mollusc from Hawaii. *Pacific Science* 15: 112–113
- Kay, E.A. (1964). A new species of *Berthelinia* and its associated sacoglossans in the Hawaiian Islands. *Proceedings of the Malacological Society of London* 36: 191–197
- Kay, E.A. (1968). A review of the bivalved gastropods and a discussion of evolution within the Sacoglossa. *Symposia of the Zoological Society of London* 22: 109–134
- Kay, E.A. (1979). Hawaiian marine shells. Reef and shore fauna of Hawaii: Section 4: Mollusca. Bernice P. Bishop Museum Special Publication 64: 1–653
- Kay, E.A. & Young, D.K. (1969). The Doridacea (Opisthobranchia; Mollusca) of the Hawaiian Islands. *Pacific Science* 23: 172–231
- Keen, A.M. & Smith, A.G. (1961). West American species of the bivalved gastropod genus *Berthelinia*. *Proceedings of the California Academy of Sciences* (4) 30: 47–66
- Kempf, S. (1981). Long-lived larvae of the gastropod *Aplysia juliana*: do they disperse and metamorphose or just slowly fade away? *Marine Ecology Progress Series* 6: 61–65
- Kitao, K. & Habe, T. (1982). Systematic positions of *Hamineobulla kawamurai* Habe, 1950 and *Pseudophilina hayashi* Habe, 1976. *Venus* 41: 61–63
- Kress, A. (1977). *Runcina ferruginea* n.sp. (Cephalaspidea: Opisthobranchia: Gastropoda), a new runcinid from Great Britain. *Journal of the Marine Biological Association of the United Kingdom* 57: 201–211
- Kress, A. (1985a). A structural analysis of the spermatophore of *Runcina ferruginea* Kress (Opisthobranchia: Cephalaspidea). *Journal of the Marine Biological Association of the United Kingdom* 65: 337–342
- Kress, A. (1985b). The male copulatory apparatus in an opisthobranch mollusc, *Runcina*. *Tissue and Cell* 17: 215–226
- Kriegstein, A.R., Castelluci, V. & Kandel, E.R. (1974). Metamorphosis of *Aplysia californica* in laboratory culture. *Proceedings of the National Academy of Sciences of the United States of America* 71: 3654–3658
- Kuroda, T., Habe, T. & Oyama, K. (1971). *The Sea Shells of Sagami Bay collected by His Majesty the Emperor of Japan*. Maruzen : Tokyo xvi 741 pp., 489 pp., 51 pp., 121 pls
- Kuzirian, A.M. (1979). Taxonomy and biology of four New England coryphellid nudibranchs (Gastropoda: Opisthobranchia). *Journal of Molluscan Studies* 45: 239–261
- Lacaze-Duthiers, H. (1859). Histoire anatomique et physiologique du pleurobranche orangé. *Annales des Sciences Naturelles* 11: 199–302
- Lalli, C.M. (1970a). Structure and function of the buccal apparatus of *Clione limacina* (Phipps), with a review of feeding in gymnosomatous pteropods. *Journal of Experimental Marine Biology and Ecology* 4: 101–118
- Lalli, C.M. (1970b). Morphology of *Crucibranchaea macrochira* (Meisenheimer), a gymnosomatous pteropod. *Proceedings of the Malacological Society of London* 39: 1–14
- Lalli, C.M. (1972). Food and feeding of *Paedoclione doliiformis* Danforth, a neotenous gymnosomatous pteropod. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 143: 392–402
- Lalli, C.M. & Conover, R.J. (1973). Reproduction and development of *Paedoclione doliiformis*, and a comparison with *Clione limacina* (Opisthobranchia: Gymnosomata). *Marine Biology* 19: 13–22
- Lalli, C.M. & Conover, R.J. (1976). Microstructure of the veliger shells of gymnosomatous pteropods. *The Veliger* 18: 237–240
- Lalli, C.M. & Gilmer, R.W. (1989). *Pelagic Snails. The Biology of Holoplanktonic Gastropod Mollusks*. Stanford University Press : Stanford, California xiv 259 pp.
- Lalli, C.M. & Wells, F.E. (1973). Brood protection in an epipelagic thecosomatous pteropod, *Spiratella* ("Limacina") *inflata* (d'Orbigny). *Bulletin of Marine Science* 23: 933–941

- Lalli, C.M. & Wells, F.E. (1978). Reproduction in the genus *Limacina* (Opisthobranchia: Thecosomata). *Journal of Zoology, London* 186: 95–108
- Lance, J.R. (1962). A new species of *Armina* (Gastropoda: Nudibranchia) from the Gulf of California. *The Veliger* 5: 51–54
- Le Brasseur, R.J. (1966). Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. *Journal of the Fisheries Research Board of Canada* 23: 85–100
- Lebour, M.V. (1931). *Clione limacina* in Plymouth waters. *Journal of the Marine Biological Association of the United Kingdom* 17: 785–795
- Lebour, M.V. (1932). *Limacina retroversa* in Plymouth waters. *Journal of the Marine Biological Association of the United Kingdom* 18: 123–129
- Lederhendler, I.I. (1977a). Reproductive behavior of *Aplysia dactylomela* (Rang, 1828) (Opisthobranchia: Gastropoda). PhD thesis, City University, New York 161 pp.
- Lederhendler, I.I. (1977b). The development of conspecific interactions in juvenile *Aplysia dactylomela* Rang, 1828: an observational study. *The Veliger* 20: 173–178
- Lederhendler, I.I. & Tobach, E. (1977). Reproductive roles in the simultaneous hermaphrodite *Aplysia dactylomela*. *Nature* 270: 238–239
- Lemche, H. (1948). Northern and Arctic tectibranch gastropods. I. The larval shells. II. A revision of the cephalaspid species. *Biologiske Skrifter. Det Kongelige Danske Videnskabernes Selskab* 5(3): 1–136
- Lemche, H. (1956). The anatomy of the histology of *Cylindrina* (Gastropoda Tectibranchia). *Spolia Zoologica Musei Hauniensis* 16: 1–278
- Lemche, H. (1974). The teeth of three bivalved gastropods and three other species of the order Sacoglossa. Appendix: *Calliopaea oophaga* n. sp., a new sacoglossan. *Proceedings of the Malacological Society of London* 41: 124–126
- Lewin, R.A. (1970). Toxin secretion and tail autotomy in irritated *Oxynoe panamensis* (Opisthobranchia, Sacoglossa). *Pacific Science* 24: 356–358
- Lin, G. (1978). A new species of *Cylindrobulla* (Opisthobranchia) of the Xisha Islands, Guangdong Province, China. *Oceanologia et Limnologia Sinica* 9: 95–98
- Lin, G. (1980). A new genus and species of Ringiculidae. *Oceanologia et Limnologia Sinica* 11: 263–266
- Lin, G. (1989). A study on Acteonidae (Opisthobranchia) from China coast. *Studia Marina Sinica* 30: 167–176
- Lloyd, H.M. (1952). A study of the reproductive system of some opisthobranch molluscs. PhD Thesis, University of London, London 107 pp.
- Loch, I. (1989). Sailors eyeballs – the inside story. *Australian Shell News* No. 68: 5–6
- Ludbrook, N.H. (1958). The molluscan fauna of the Pliocene Strata underlying the Adelaide Plains, Part V – Gastropoda (Eratoidae to Scaphandridae). *Transactions of the Royal Society of South Australia* 81: 43–111
- Ludbrook, N.H. (1978). Quaternary molluscs of the western part of the Eucla Basin. *Bulletin of the Geological Survey of Western Australia* 125: 1–286
- Ludbrook, N.H. (1984). Quaternary molluscs of South Australia. *Department of Mines and Energy, South Australia, Handbook* No. 9: 1–327
- Ludbrook, N.H. & Steel, T.M. (1961). A late Tertiary bivalve gastropod from South Australia. *Proceedings of the Malacological Society of London* 34: 228–230
- Luque, A.A. (1983). Contribucion al conocimiento de los gasteropodos de las costas de Malaga y Granada. I. Opisthobranchios (1). *Iberius* 3: 51–74
- MacFarland, F.M. (1923). The morphology of the nudibranch genus *Hancockia*. *Journal of Morphology* 38: 65–104
- MacFarland, F.M. (1966). Studies of opisthobranchiate mollusks of the Pacific Coast of North America. *Memoirs of the California Academy of Science* 6: 1–546
- Macnae, W. (1958). The families Polyceridae and Goniodorididae (Mollusca, Nudibranchiata) in southern Africa. *Transactions of the Royal Society of South Africa* 35: 341–372
- Macnae, W. (1962). Tectibranch molluscs from southern Africa. *Annals of the Natal Museum* 15: 183–199
- Macpherson, J.H. & Gabriel, C.J. (1962). *Marine Molluscs of Victoria*. Melbourne University Press & National Museum of Victoria: Melbourne xv 475 pp.
- Maes, V.O. (1967). The littoral marine mollusks of Cocos-Keeling Islands (Indian Ocean). *Proceedings of the Academy of Natural Sciences of Philadelphia* 119: 93–217
- Mancino, G. & Sordi, M. (1964). Il corredo cromosomico di Nudibranchi ed Ascoglossi (Gasteropodi, Opisthobranchi) del Mar Tirreno. *Atti della Accademia Nazionale dei Lincei. Rendiconti della Classe di Scienze Fisiche, Matematiche e Naturali* (8) 37: 496–500
- Marbach, A. & Tsumamal, M. (1973). On the biology of *Berthellina citrina* (Gastropoda: Opisthobranchia) and its defensive acid secretion. *Marine Biology* 21: 331–339
- Marcus, Er. (1953). Three Brazilian sand-Opisthobranchia. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia* 18: 165–203
- Marcus, Er. (1955). Opisthobranchia from Brazil. *Boletim da Faculdade de Filosofia Ciências e Letras da Universidade de São Paulo, Zoologia* 20: 89–261
- Marcus, Er. (1957). On Opisthobranchia from Brazil (2). *Journal of the Linnean Society of London (Zoology)* 43: 390–486
- Marcus, Er. (1958a). On western Atlantic opisthobranchiate gastropods. *American Museum Novitates* 1906: 1–82
- Marcus, Er. (1958b). Notes on Opisthobranchia. *Boletim do Instituto Oceanografico, Universidade de São Paulo* 7: 31–78 [publication dated 1956]
- Marcus, Er. (1959). Eine neue Gattung der Philinoglossacea. *Kieler Meeresforschungen* 15: 117–119
- Marcus, Er. (1965). Some Opisthobranchia from Micronesia. *Malacologia* 3: 263–286
- Marcus, Er. & Burch, J.B. (1965). Marine euthyneuran Gastropoda from Eniwetok Atoll, Western Pacific. *Malacologia* 3: 235–262
- Marcus, Er. & Marcus, Ev. du B.-R. (1960). Opisthobranchia aus dem Roten Meer und von dem Malediven. *Akademie der Wissenschaften und der Literatur. Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse NR* 12: 873–933
- Marcus, Er. & Marcus Ev. du B.-R. (1970). Opisthobranchs from Curaçao and faunistically related regions. *Studies on the Fauna of Curaçao and other Caribbean Islands* 33: 1–129
- Marcus, Ev. du B.-R. (1970). Opisthobranchs from northern Brazil. *Bulletin of Marine Science* 20: 922–951
- Marcus, Ev. du B.-R. (1972a). On some Acteonidae (Gastropoda, Opisthobranchia). *Papéis Avulsos de Zoologia, São Paulo* 25: 167–188
- Marcus, Ev. du B.-R. (1972b). Notes on some opisthobranch gastropods from Chesapeake Bay. *Chesapeake Science* 13: 300–317
- Marcus, Ev. du B.-R. (1972c). On some opisthobranchs from Florida. *Bulletin of Marine Science* 22: 284–308
- Marcus, Ev. du B.-R. (1972d). On the Anaspidea (Gastropoda: Opisthobranchia) of the warm waters of the western Atlantic. *Bulletin of Marine Science* 22: 841–874
- Marcus, Ev. du B.-R. (1973). On the genus *Bosellia* (Mollusca: Gastropoda: Ascoglossa). *Bulletin of Marine Science* 23: 811–823
- Marcus, Ev. du B.-R. (1974). On some Cephalaspidea (Gastropoda: Opisthobranchia) from the western and middle Atlantic warm waters. *Bulletin of Marine Science* 24: 300–371
- Marcus, Ev. du B.-R. (1976). A taxonomic survey of the genus *Toledonia* Dall, 1902 (Opisthobranchia, Diaphanidae). *Zoologica Scripta* 5: 25–33
- Marcus, Ev. du B.-R. (1977). On the genus *Tornatina* and related forms. *Journal of Molluscan Studies, Supplement* No. 2: 1–35
- Marcus, Ev. du B.-R. (1978). On a new species of *Bosellia*. *Boletim de Zoologia, Universidade de São Paulo* 3: 1–6

16. OPISTHOBRANCHIA

- Marcus, Ev. du B.-R. (1980). Review of Western Atlantic Elysiidae (Opisthobranchia Ascoglossa) with a description of a new *Elysia* species. *Bulletin of Marine Science* 30: 54–79
- Marcus, Ev. du B.-R. (1982). Systematics of the genera of the order Ascoglossa (Gastropoda). *Journal of Molluscan Studies, Supplement* 10: 1–31
- Marcus, Ev. du B.-R. (1985). Catalogue of the Western Atlantic warm water Opisthobranchia. 10. The Western Atlantic warm water Notaspidea (Gastropoda: Opisthobranchia), Part 3. Umbraculacea. *Boletim de Zoologia* 9: 1–15
- Marcus, Ev. du B.-R. & Marcus, Er. (1954). Über Philinoglossacea und Acochliidae. *Kieler Meeresforschungen* 10: 215–223
- Marcus, Ev. du B.-R. & Marcus, Er. (1956a). On the tectibranch gastropod *Cylindrobulla*. *Anais da Academia Brasileira de Ciências* 28: 119–130
- Marcus, Ev. du B.-R. & Marcus, Er. (1956b). On two sacoglossan slugs from Brazil. *American Museum Novitates* 1796: 1–21
- Marcus, Ev. du B.-R. & Marcus, Er. (1958). Opisthobranchia aus dem Schill von Helgoland. *Kieler Meeresforschungen* 14: 91–96
- Marcus, Ev. du B.-R. & Marcus, Er. (1960). Opisthobranchs from American Atlantic warm waters. *Bulletin of Marine Science of the Gulf and Caribbean* 10: 129–203
- Marcus, Ev. du B.-R. & Marcus, Er. (1966b). The R/V Pillsbury deep-sea biological expedition to the Gulf of Guinea, 1964–65. 9. Opisthobranchs from tropical West Africa. *Studies in Tropical Oceanography* 4: 152–208
- Marcus, Ev. du B.-R. & Marcus, Er. (1967a). Opisthobranchs from the southwestern Caribbean Sea. *Bulletin of Marine Science* 17: 597–628
- Marcus, Ev. du B.-R. & Marcus, Er. (1967b). American opisthobranch mollusks. *Studies in Tropical Oceanography* No. 6: 1–256
- Marcus, Ev. du B.-R. & Marcus, Er. (1969a). Opisthobranchian and lamellarian gastropods collected by the 'Vema. *American Museum Novitates* 2368: 1–33
- Marcus, Ev. du B.-R. & Marcus, Er. (1969b). Euthyneure Meeresschnecken Brasiliens (2). *Beiträge zur Neotropischen Fauna* 6: 1–16
- Marcus, Ev. du B.-R. & Marcus, Er. (1970). Some gastropods from Madagascar and west Mexico. *Malacologia* 10: 181–223
- Martin, R. (1966). On the swimming behaviour and biology of *Notarchus punctatus* Philippi (Gastropoda, Opisthobranchia). *Pubblicazioni della Stazione Zoologica di Napoli* 35: 61–75
- Martin, R. & Brinckmann, A. (1936). Zum Brutparasitismus von *Phyllirhoe bucephala* Per. & Les. (Gastropoda, Nudibranchia) auf der Meduse *Zanclea costata* Gegenb. (Hydrozoa, Anthomedusae). *Pubblicazioni Stazione Zoologica di Napoli* 33: 206–223
- Martoja, M. (1965). Sur l'incubation et l'existence possible d'une glande endocrine, chez *Hydromyles globulosa* Rang, gastéropode gymnosome (*Halopsyche gaudichaudi* Keferstein). *Comptes Rendus Hebdomadaire des Séances de l'Académie Sciences* 260: 2907–2909
- Massy, A.L. (1917). The gymnosomatous Pteropoda of the coasts of Ireland. *Science Proceedings of the Royal Dublin Society (ns)* 15: 223–244
- Mayeri, E., Koester, J., Kupfermann, I., Liebeswar, G. & Kandel, E.R. (1974). Neural control of circulation in *Aplysia* I: Motoneurons. *Journal of Neurophysiology* 37: 458–475
- McDonald, G.R. & Nybakken, J.W. (1980). *Guide to the Nudibranchs of California - including most species found from Alaska to Oregon*. American Malacologists Inc.: Melbourne, Florida 72 pp.
- Meisenheimer, J. (1904). Zur Anatomie und systematischen stellung von *Desmopterus papilio* Chun. *Zoologischer Anzeiger* 27: 331–334
- Meisenheimer, J. (1905). Pteropoda. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 9: 1–314
- Mikkelsen, P.M. & Mikkelsen, P.S. (1987). Redescription of *Acteocina recta* and *A. lepta*, two species of cephalaspidean gastropods from the western Atlantic. *The Nautilus* 101: 51–58
- Mikkelsen, P.S. & Mikkelsen, P.M. (1984). Comparison of *Acteocina canaliculata* (Say, 1826), *A. candei* (d'Orbigny, 1841) and *A. atrata* sp. nov. (Gastropoda: Cephalaspidea). *The Veliger* 27: 164–192
- Mileikovsky, S.A. (1970). Breeding and larval distribution of the pteropod, *Clione limacina* in the North Atlantic, Subarctic and North Pacific Oceans. *Marine Biology* 6: 317–334
- Millen, S.M. (1985). The nudibranch genera *Onchidoris* and *Diaphorodoris* (Mollusca: Opisthobranchia) in the Northeastern Pacific. *The Veliger* 28: 80–93
- Miller, M.C. (1969). The habits and habitats of the opisthobranch molluscs of the British Solomon Islands. *Philosophical Transactions of the Royal Society of London, Series B* 255: 541–548
- Miller, M.C. (1970). Two new species of the genus *Caldukia* Burn & Miller, 1969 (Mollusca: Gastropoda: Opisthobranchia) from New Zealand waters. *The Veliger* 12: 279–289
- Miller, M.C. (1971). Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Flabellinidae and Eubranichidae from New Zealand waters. *Zoological Journal of the Linnean Society* 50: 311–337
- Miller, M.C. (1974). Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Glaucidae from New Zealand waters. *Zoological Journal of the Linnean Society* 54: 31–61
- Miller, M.C. (1977). Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Tergipedidae from New Zealand waters. *Zoological Journal of the Linnean Society* 60: 197–222
- Miller, M.C. (1980). Predator or prey: nudibranchs and coelenterates. *Journal of the Malacological Society of Australia* 4: 239–240
- Miller, M.C. & Rudman, W.B. (1968). Two new genera and species of the superfamily Runcinoidea (Mollusca: Gastropoda: Opisthobranchia) from New Zealand. *Transactions of the Royal Society of New Zealand (Zoology)* 10: 183–189
- Miller, M.C. & Willan, R.C. (1986). A review of the New Zealand arminacean nudibranchs (Opisthobranchia: Arminacea). *New Zealand Journal of Zoology* 13: 377–408
- Miller, M.C. & Willan, R.C. (1991). Redescription of *Embletonia gracile* Risbec, 1928 (Nudibranchia: Embletoniidae): relocation to suborder Dentronotacea taxonomic and phylogenetic implications. *Journal of Molluscan Studies* 58: 1–12
- Mimoto, K. (1984). *Julia* (bivalved Gastropoda) from the Pleistocene deposits of Kikai-jima, the Amami Islands. *Chiribotan* 14: 87–88
- Minichev, Y.S. (1966). Morphological peculiarities of abyssal Cephalaspidea (Gastropoda, Opisthobranchia). *Zoologicheskii Zhurnal* 45: 509–517
- Minichev, Y.S. (1967). Studies on the morphology of the lower Opisthobranchia. On the evolutionary significance of the detorsion process. *Proceedings of the Zoological Institute of the Academy of Sciences of the USSR* 44: 109–182
- Minichev, Y.S. (1971). On the fauna, ecology and systematics of the Retusidae (Opisthobranchia Cephalaspidea) of Possjet Bay in the Sea of Japan. *Issledovaniya Fauny Morei, Leningrad* 8: 230–241
- Minichev, Y.S. & Starobogatov, Y.I. (1978). On the systematic arrangement of euthyneuran snails. *Malacological Review* 11: 67–68
- Minichev, Y.S. & Starobogatov, Y.I. (1979a). The sub-classes of Gastropoda and their phylogenetic relations. *Zoologicheskii Zhurnal* 58: 293–305
- Minichev, Y.S. & Starobogatov, Y.I. (1979b). Peculiarities of the evolution of the reproductive system of the Opisthobranchia and their taxonomy. Pp. 16–20 in Likharev, I.M. (ed.) *Sixth meeting on the Investigation of Molluscs. Mollusca. Main results of their study. Abstracts of Communications*. Nauka: Leningrad,
- Minichev, Y.S. & Starobogatov, Y.I. (1984). Taxonomy of Opisthobranchia and peculiarities of the evolution of the reproductive system. *Malacological Review* 17: 112–114
- Moquin-Tandon, M.G. (1870). Recherches anatomiques sur l'Ombrelle de la Méditerranée. *Annales des Sciences Naturelles (Zoologie et Paleontologie)* 14: 1–135

- Morrow, C.C., Thorpe, J.P. & Picton, B.E. (1992). Genetic divergence and cryptic speciation in two morphs of the common subtidal nudibranch *Doto coronata* (Opisthobranchia: Dendronotacea: Dotoidea) from the northern Irish Sea. *Marine Ecology Progress Series* 84: 53–61
- Morse, M.P. (1984). Functional adaptations of the digestive system of the carnivorous mollusc *Pleurobranchaea californica* MacFarland, 1966. *Journal of Morphology* 180: 253–269
- Morton, B. & Chiu, S.T. (1990). The diet, prey size and consumption of *Philine orientalis* (Opisthobranchia: Philinidae) in Hong Kong. *Journal of Molluscan Studies* 56: 289–299
- Morton, J.E. (1954). The biology of *Limacina retroversa*. *Journal of the Marine Biological Association of the United Kingdom* 33: 297–312
- Morton, J.E. (1958a). Observations on the gymnosomatous pteropod *Clione limacina* (Phipps). *Journal of the Marine Biological Association of the United Kingdom* 37: 287–297
- Morton, J.E. (1958b). *Molluscs*. Hutchinson University Library: London 232 pp.
- Morton, J.E. (1972). The form and functioning of the pallial organs in the opisthobranch *Akera bullata* with a discussion on the nature of the gill in Notaspidea and other tectibranchs. *The Veliger* 14: 337–349
- Morton, J.E. (1979). *Molluscs*. Hutchinson: London 5th edn 264 pp.
- Morton, J.E. & Holme, N.A. (1955). The occurrence at Plymouth of the opisthobranch *Akera bullata*, with notes on its habits and relationships. *Journal of the Marine Biological Association of the United Kingdom* 34: 101–112
- Morton, J.E. & Miller, M.C. (1968). *The New Zealand Sea Shore*. Collins: London 638 pp.
- Murray, M.J. & Lewis, E.R. (1974). Sensory control of prey capture in *Navanax inermis*. *The Veliger* 17: 156–158
- Myers, T.D. (1968). Horizontal and vertical distribution of thecosomatous pteropods off Cape Hatteras. PhD Thesis, Duke University, North Carolina 224 pp. place
- Newman, L.J. (1990). Holoplanktonic molluscs (Gastropoda; Thecosomata, Gymnosomata and Heteropoda) from the waters of Australia and Papua New Guinea: Their taxonomy, distribution and biology. PhD thesis, University of Queensland, Brisbane 208 pp.
- Newman, L.J. & Corey, S. (1984). Aspects of the distribution and biology of pteropods (Gastropoda, Opisthobranchia) from the Bay of Fundy region, Canada. *Canadian Journal of Zoology* 62: 397–404
- Newman, L.J. & Greenwood, J.G. (1987). First records of the pteropods *Clio scheelei* (Munthe, 1888) and *Clio andreae* (Boas, 1886) (Opisthobranchia: Thecosomata) from the western Pacific Ocean. *The Veliger* 30: 90–94
- Newman, L.J. & Greenwood, J.G. (1988). A new species of gymnosome, *Pneumodermopsis spoeli* (Gastropoda: Opisthobranchia) from the Great Barrier Reef, Australia. *The Veliger* 31: 75–79
- Newman, L.J. & van der Spoel, S. (1989). *Pneumoderma heronensis* nov. sp., a new pteropod (Opisthobranchia; Gymnosomata) from Australian waters. *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 12: 81–85
- Nishimura, S. (1965). Droplets from the plankton net, XX. 'Sea stings' caused by *Creseis acicula* Rang (Mollusca: Pteropoda) in Japan. *Publications of the Seto Marine Biological Laboratory* 13: 287–290
- Nolen, T.G., Johnson, P.M., Kicklighter, C.E. & Capo, T. (1995). Ink secretion by the marine snail *Aplysia californica* enhances its ability to escape from a natural predator. *Journal of Comparative Physiology (A)* 176: 239–254
- O'Donoghue, C.H. (1929). Opisthobranchiate mollusca collected by the South African Marine Biological Survey. *Reports of the Fisheries and Marine Biological Survey, South Africa* 7: 1–84
- Odhner, N.H. (1914). *Pisanula limnaeoides*, a new Arctic opisthobranchiate mollusc, its anatomy and affinities. *Arkiv för Zoologi* 8: 1–18
- Odhner, N.H. (1924). New Zealand Mollusca. (Papers from Dr Th. Mortensen's Pacific Expedition 1914–16 XIX). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 77: 1–90
- Odhner, N.H. (1926). Die Opisthobranchien. *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903* 2: 1–100
- Odhner, N.H. (1934). The Nudibranchiata. British Antarctic ("Terra Nova") Expedition 1910. *British Museum Natural History Report, Zoology* 7: 229–310
- Odhner, N.H. (1936). Nudibranchia Dendronotacea. A revision of the system. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* (2) 3: 1057–1128
- Odhner, N.H. (1939). Opisthobranchiate Mollusca from the western and northern coasts of Norway. *Kongelige Norske Videnskabernes Selskabs Skrifter NR* No. 1: 1–93
- Odhner, N.H. (1941). New polycerid nudibranchiate mollusca and remarks on this family. *Meddelanden från Göteborgs Musei Zoologiska Ardelning* 91: 1–20
- Odhner, N.H. (1952). Petits opisthobranches peu connus de la côte Méditerranéenne de France. *Vie et Milieu* 3: 136–147
- Odhner, N.H. (1963). On the taxonomy of the family Tritoniidae (Mollusca: Opisthobranchia). *The Veliger* 6: 48–52
- Odhner, N.H. (1968). Sous-classe des Opisthobranches. Systématique. Pp. 834–888 in Grassé, P.P. (ed.) *Traité de Zoologie. Vol. 5. Pt 3. Mollusques Gastéropodes et Scaphopodes*. Masson et Cie: Paris
- Odhner, N.H. (1973). On the taxonomy of the family Tritoniidae (Mollusca: Opisthobranchia). *The Veliger* 6: 48–51
- Ortea, J. (1981). Moluscos opisthobranchios de las Islas Canarias. Primera parte: Ascoglossos. *Boletín do Instituto Espanol Oceanografico* 6: 179–199
- Ortea, J., Bacallado, J.J. & Pérez Sánchez, J.M. (1990). *Aplysiopsis formosa* Pruvot-Fol, 1953 (Mollusca, Opisthobranchia, Ascoglossa) in the Canary Islands. *Lavori della Società Italiana di Malacologia* 23: 281–285
- Pace, S. (1901). On the rediscovery of *Euselenops* (= *Neda*) *luniceps* (Cuv.). *Proceedings of the Malacological Society of London* 4: 202–204
- Pafort-van Iersel, T. & van der Spoel, S. (1986). Schizogamy in the planktonic opisthobranch *Clio* – a previously undescribed mode of reproduction in the Mollusca. *International Journal of Invertebrate Reproduction and Development* 10: 43–50
- Paige, J.A. (1986). The laboratory culture of two aplysiids, *Aplysia brasiliensis* Rang, 1828, and *Bursatella leachii* plei (Rang, 1828) (Gastropoda: Opisthobranchia) in artificial seawater. *The Veliger* 29: 64–69
- Paine, R.T. (1963). Food recognition and predation on opisthobranchs by *Navanax inermis* (Gastropoda: Opisthobranchia). *The Veliger* 6: 1–9
- Pauly, D. & Calumpong, H. (1984). Growth, reproduction and mortality of the sea hare *Dolabella auricularia* (Gastropoda: Aplysiidae) in the central Visayas, Philippines. *Marine Biology* 79: 289–293
- Pease, W.H. (1860). Descriptions of new species of Mollusca from the Sandwich Islands, Part 1. *Proceedings of the Zoological Society of London* 1860: 18–36
- Pease, W.H. (1871). Descriptions of nudibranchiate Mollusca inhabiting Polynesia. *American Journal of Conchology* 6: 299–305
- Pelseneer, P. (1887). Report on the Pteropoda collected by H.M.S. *Challenger* during the years 1873–76. Part I. The Gymnosomata. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873–76, Zoology* 19: 1–74
- Pelseneer, P. (1888a). Report on the Pteropoda collected by H.M.S. *Challenger*, during the years 1873–1876. Part III – Anatomy. *Scientific Results of the Voyage of H.M.S. Challenger, Zoology* 23 (46): 1–97
- Pelseneer, P. (1888b). Report on the Pteropoda collected by the H.M.S. *Challenger* during the years 1873–1876. II. The Thecosomata. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873–76, Zoology* 23: 1–132
- Pelseneer, P. (1894). Recherches sur divers Opisthobranches. *Mémoires Couronnés et Mémoires des Savants Étrangers* 53: 1–157

16. OPISTHOBRANCHIA

- Pelseneer, P. (1925). Organisation et position systématique du genre *Ringicula*. *Annales de la Société Royale Malacologique Belgique* 55: 53–58
- Perrier, R. & Fischer, H. (1911). Recherches anatomiques et histologiques sur la cavité palléale et ses dépendances chez les Bulléens. *Annales des Sciences Naturelles (Zoologie)* 14: 1–190
- Perron, F.E. & Turner, R.D. (1977). Development, metamorphosis, and natural history of the nudibranch *Doridella obscura* Verrill (Corambidae: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology* 27: 171–185
- Pilsbry, H.A. (1895). Tectibranchiata. In Tryon, G.W. *Manual of Conchology* 15: 134–436
- Plant, F. (1977). Tropical gastropods found in Spencers Gulf, South Australia. *Australian Shell News* No. 18: 6
- Platts, E. (1985). North Atlantic nudibranchs (Mollusca) seen by Henning Lemche, with additional species from the Mediterranean and north east Pacific. Appendix: an annotated list of the north Atlantic Opisthobranchia. *Ophelia* Supplement No. 3: 150–170
- Poizat, C. (1978). Recherches des paramètres écologiques favorables à l'existence du gastéropode opisthobranch Acochlidacea, *Platyhedyle* Salvini-Plawen, 1973, dans les sédiments marins des environs de Marseille. *Haliotis* 7: 31–38
- Ponder, W.F. (1987). The anatomy and relationships of the pyramidellacean limpet *Amathina tricarinata* (Mollusca: Gastropoda). *Asian Marine Biology* 4: 1–34
- Ponder, W.F. & Lindberg, D.R. (1996). Gastropod phylogeny – challenges for the 90s. Pp. 135–154 in Taylor, J.D. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press: Oxford
- Ponder, W.F. & Warén, A. (1988). Classification of the Caenogastropoda and Heterostrophia – a list of the family group names and higher taxa. Pp. 288–328 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement* 4
- Poorman, L.H. & Mulliner, D.K. (1981). A new species of *Crosslandia* (Nudibranchia: Dendronotacea) from the Gulf of California. *The Nautilus* 95: 96–99
- Powell, A.W.B. (1951). Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. *Discovery Reports* 26: 47–196
- Powell, A.W.B. (1960). Antarctic and Subantarctic Mollusca. *Records of the Auckland Institute and Museum* 5: 117–193
- Powell, A.W.B. (1979). *New Zealand Mollusca: Marine, Land and Freshwater Shells*. Collins: Auckland 500 pp.
- Pruvot-Fol, A. (1924). Étude de quelques gymnosomes méditerranéens des pêches de l'"Orvet" en 1921 et 1922. *Archives de Zoologie Expérimentale et Générale* 62: 345–400
- Pruvot-Fol, A. (1935). Les doridiens de Cuvier. *Journal de Conchyliologie* 78: 209–261
- Pruvot-Fol, A. (1942). Les Gymnosomes I. *Dana Report* 4: 1–54
- Pruvot-Fol, A. (1954). Mollusques Opisthobranches. *Faune de France* 58: 1–460
- Quoy, J.R.C. & Gaimard, J.P. (1830–1834). *Voyages de découvertes de l'Astrolabe exécuté par ordre du Roi pendant les années 1826–1827–1828–1829 sous le commandement de M.J. Dumont d'Urville*. *Zoologie* 2: 1–686
- Ralph, P.M. (1944). *Pellibranchus cinnabareus*, a new genus and species of non-pelagic nudibranch mollusc of the family Phylliriodae. *Transactions of the Royal Society of New Zealand* 74: 24–31
- Rankin, J.J. (1979). A freshwater shell-less mollusc from the Caribbean: structure, biotics, and contribution to a new understanding of the Acochlidioidea. *Contributions. Life Sciences Division, Royal Ontario Museum* No. 116: 1–123
- Rasmussen, E. (1944). Faunistic and biological notes on marine invertebrates I. The eggs and larvae of *Brachystomia rissoides* (Hanl.), *Eulimella nitidissima* (Mont.), *Retusa trunculata* (Brug.) and *Embletonia pallida* (Alder & Hancock), (Gastropoda marina). *Videnskabelige Meddeleser fra Dansk Naturhistorisk Forening, København* 107: 207–233
- Raymond, B.G. & Bleakney, J.S. (1987). The radular and ascus of *Elysia chlorotica* Gould (Opisthobranchia: Ascoglossa). *The Veliger* 29: 245–250
- Redfield, A.C. (1939). The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biological Bulletin, Marine Biological Laboratory Woods Hole* 76: 26–47
- Rehder, H.A. (1980). The marine mollusks of Easter Island (Isla de Pascua) and Sala y Gómez. *Smithsonian Contributions to Zoology* 289: 1–167
- Reid, J.D. (1964). The reproduction of the sacoglossan opisthobranch *Elysia maoria*. *Proceedings of the Zoological Society of London* 143: 365–393
- Riley, G.A. (1963). Organic aggregates in sea water and the dynamics of their formation and utilization. *Limnology and Oceanography* 8: 372–381
- Risbec, J. (1928). Contribution à l'étude des nudibranches Néo-Calédoniens. In *Faune des Colonies Françaises* 2(1): 1–328
- Risbec, J. (1953). *Mollusques Nudibranches de la Nouvelle-Calédonie*. Faune Union Française. Office de la Recherche Scientifique Outre-Mer 15: 1–189
- Robles, L.J. (1975). The anatomy and functional morphology of the reproductive systems of *Bulla gouldiana* (Gastropoda: Opisthobranchia). *The Veliger* 17: 278–291
- Rose, R.A. (1985). The spawn and development of twenty-nine New South Wales opisthobranchs (Mollusca: Gastropoda). *Proceedings of the Linnean Society of New South Wales* 108: 23–36
- Rose, R.A. & Hoegh-Guldberg, I.O. (1982). A brood protecting nudibranch with pelagic lecithotrophic development. *Journal of Molluscan Studies* 48: 231–232
- Rudman, W.B. (1970). *Chelidonura inornata* Baba and *C. electra* sp. nov. from the Solomon Islands (Opisthobranchia, Aglajidae). *Journal of the Malacological Society of Australia* 2: 7–12
- Rudman, W.B. (1971a). On the opisthobranch genus *Haminoea* Turton & Kingston. *Pacific Science* 25: 545–559
- Rudman, W.B. (1971b). Structure and functioning of the gut in the Bullomorpha (Opisthobranchia). Part 1. Herbivores. *Journal of Natural History* 5: 647–675
- Rudman, W.B. (1971c). The family Acteonidae (Opisthobranchia: Gastropoda) in New Zealand. *Journal of the Malacological Society of Australia* 2: 205–214
- Rudman, W.B. (1971d). The genus *Bullina* (Opisthobranchia, Gastropoda) in New Zealand. *Journal of the Malacological Society of Australia* 2: 195–203
- Rudman, W.B. (1971e). On a new genus for "*Tornatina*" murchisoni Suter, 1913 (Retusidae, Opisthobranchia). *Journal of the Malacological Society of Australia* 2: 187–193
- Rudman, W.B. (1972a). The anatomy of the opisthobranch genus *Hydatina* and the functioning of the mantle cavity and alimentary canal. *Zoological Journal of the Linnean Society* 51: 121–139
- Rudman, W.B. (1972b). A study of the anatomy of *Pupa* and *Maxacteon* (Acteonidae, Opisthobranchia), with an account of the breeding cycle of *Pupa kirki*. *Journal of Natural History* 6: 603–619
- Rudman, W.B. (1972c). On *Melanochlamys* Cheeseman, 1881, a genus of the Aglajidae (Opisthobranchia, Gastropoda). *Pacific Science* 26: 50–62
- Rudman, W.B. (1972d). Structure and functioning of the gut in the Bullomorpha (Opisthobranchia). Part 4. Aglajidae. *Journal of Natural History* 6: 547–560
- Rudman, W.B. (1972e). Structure and functioning of the gut in the Bullomorpha (Opisthobranchia). Part 3. Philinidae. *Journal of Natural History* 6: 459–474; - in text as 1971h
- Rudman, W.B. (1972f). The genus *Philine* (Opisthobranchia, Gastropoda). *Proceedings of the Malacological Society of London* 40: 171–187
- Rudman, W.B. (1972g). The herbivorous opisthobranch genera *Phanerophthalmus* A. Adams and *Smaragdinella* A. Adams. *Proceedings of the Malacological Society of London* 40: 189–210
- Rudman, W.B. (1972h). Structure and functioning of the gut in the Bullomorpha (Opisthobranchia). Part 2. Acteonidae. *Journal of Natural History* 6: 311–324

- Rudman, W.B. (1972i). Studies on the primitive opisthobranch genera *Bullina* Férussac and *Micromelo* Pilsbry. *Zoological Journal of the Linnean Society* 51: 105–119
- Rudman, W.B. (1972j). A comparative study of the genus *Philinopsis* Pease, 1860 (Aglajidae, Opisthobranchia). *Pacific Science* 26: 381–399
- Rudman, W.B. (1973). On some species of *Chelidonura* (Opisthobranchia: Aglajidae) from Zanzibar and Fiji. *Zoological Journal of the Linnean Society* 52: 201–215
- Rudman, W.B. (1974). A comparison of *Chelidonura*, *Navanax* and *Aglaja* with the other genera of the Aglajidae (Opisthobranchia: Gastropoda). *Zoological Journal of the Linnean Society* 54: 185–212
- Rudman, W.B. (1978). A new species and genus of the Aglajidae and the evolution of the philinean opisthobranch molluscs. *Zoological Journal of the Linnean Society* 62: 89–107
- Rudman, W.B. (1979). The ecology and anatomy of a new species of aeolid opisthobranch mollusc; a predator of the scleractinian coral *Porites*. *Zoological Journal of the Linnean Society* 65: 339–350
- Rudman, W.B. (1980). Aeolid opisthobranch molluscs (Glaucidae) from the Indian Ocean and the south-west Pacific. *Zoological Journal of the Linnean Society* 68: 139–172
- Rudman, W.B. (1981a). Polyp mimicry in a new species of aeolid nudibranch mollusc. *Journal of Zoology, London* 193: 421–427
- Rudman, W.B. (1981b). Further studies on the anatomy and ecology of opisthobranch molluscs feeding on the scleractinian coral *Porites*. *Zoological Journal of the Linnean Society* 71: 373–412
- Rudman, W.B. (1981c). The anatomy and biology of alcyonarian-feeding aeolid opisthobranch molluscs and their development of symbiosis with zooxanthellae. *Zoological Journal of the Linnean Society* 72: 219–262
- Rudman, W.B. (1982a). The taxonomy and biology of further aeolidacean and arminacean nudibranch molluscs with symbiotic zooxanthellae. *Zoological Journal of the Linnean Society* 74: 147–196
- Rudman, W.B. (1982b). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris quadricolor*, *C. lineolata* and *Hypselodoris nigrolineata* colour groups. *Zoological Journal of the Linnean Society* 76: 183–241
- Rudman, W.B. (1982c). A new species of *Phestilla*, the first record of a corallivorous aeolid nudibranch from tropical America. *Journal of Zoology, London* 198: 465–471
- Rudman, W.B. (1983a). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris splendida*, *C. aspersa* and *Hypselodoris placida* colour groups. *Zoological Journal of the Linnean Society* 78: 105–173
- Rudman, W.B. (1983b). *Glossodoris* Ehrenberg, 1831, *Hypselodoris* Stimpson, 1855 and *Chromodoris* Alder & Hancock 1855 (Gastropoda, Opisthobranchia): proposed clarification and conservation. Z.N. (S.) 2432. *Bulletin of Zoological Nomenclature*, 40: 211–220
- Rudman, W.B. (1984a). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. *Zoological Journal of the Linnean Society* 81: 115–273
- Rudman, W.B. (1984b). The date and authorship of *Bornella* and *Ceratosoma* (Nudibranchia) and other molluscs collected during the voyage of *HMS Samarang*, 1843–46. *Malacological Review* 17: 103–104
- Rudman, W.B. (1985). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris aureomarginata*, *C. verrieri* and *C. fidelis* colour groups. *Zoological Journal of the Linnean Society* 83: 241–299
- Rudman, W.B. (1986a). Nudibranchs: nature's thieves. *Australian Natural History* 22: 2–7
- Rudman, W.B. (1986b). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: the genus *Glossodoris* Ehrenberg (= *Casella* H. & A. Adams). *Zoological Journal of the Linnean Society* 86: 101–184
- Rudman, W.B. (1986c). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Noumea purpurea* and *Chromodoris decora* colour groups. *Zoological Journal of the Linnean Society* 86: 309–353
- Rudman, W.B. (1986d). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Noumea flava* colour groups. *Zoological Journal of the Linnean Society* 88: 377–404
- Rudman, W.B. (1987a). Solar-powered animals. *Natural History* 96: 50–53
- Rudman, W.B. (1987b). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris epicuria*, *C. aureopurpurea*, *C. annulata*, *C. coi*, and *Risbecia tryoni* colour groups. *Zoological Journal of the Linnean Society* 90: 305–407
- Rudman, W.B. (1987c). The genus *Trapania* (Nudibranchia: Goniodorididae) in the Indo-West Pacific. *Journal of Molluscan Studies* 53: 189–212
- Rudman, W.B. (1988). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: the genus *Ceratosoma* J.E. Gray. *Zoological Journal of the Linnean Society* 93: 133–185
- Rudman, W.B. (1990a). The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: further species of *Glossodoris*, *Thorunna* and the *Chromodoris aureomarginata* colour group. *Zoological Journal of the Linnean Society* 100: 263–326
- Rudman, W.B. (1990b). *Protaeolidiella atra* Baba, 1955 and *Pleurolidia juliae* Burn, 1966; one species, two families (Nudibranchia). *Journal of Molluscan Studies* 56: 505–514
- Rudman, W.B. (1991a). Purpose in Pattern: The evolution of colour in chromodorid nudibranchs. *Journal of Molluscan Studies*, Supplement, T.E. Thompson Memorial Issue 57(4): 5–21
- Rudman, W.B. (1991b). Further studies on the taxonomy and biology of the octocoral-feeding genus *Phyllodesmium* Ehrenberg, 1831 (Nudibranchia: Aeolidioidea). *Journal of Molluscan Studies* 57: 167–203
- Rudman, W.B. & Avern, G. (1988). Molluscan dentistry; the tales that teeth tell. *Australian Natural History* 22: 388–393
- Rudman, W.B. & Avern, G.J. (1989). The genus *Rostanga* Bergh, 1879 (Nudibranchia: Dorididae) in the Indo-West Pacific. *Zoological Journal of the Linnean Society* 96: 281–338
- Rüppell, E. & Leuckart, F.S. (1828). *Neue wirbellose thiere des Rothen Meeres. Atlas zu der Reise im nordlichen Afrika von Eduard Rüppell*. Brönnner: Frankfurt 50 pp.
- Russell, F.S. & Coleman, J.S. (1935). The zooplankton. IV. The occurrence and seasonal distribution of Tunicata, Mollusca and Coelenterata (Siphonophora), Great Barrier Reef Expedition 1928–1929. *Scientific Reports on the Great Barrier Reef Expedition* 2: 235–253
- Russell, H.D. (1960). Heteropods and pteropods as food of the fish genera, *Thunnus* and *Alepisaurus*. *The Nautilus* 74: 46–56
- Russell, L. (1929). The comparative morphology of the elysiid and aeolidioid types of the molluscan nervous system, and its bearing on the relationships of the ascoglossan nudibranchs. *Proceedings of the Zoological Society of London* 14: 197–233
- Salvini-Plawen, L.v. (1973). Zur Kenntniss der Philinoglossacea und der Acochlidiacea mit Platyhedylidae fam. nov. (Gastropoda Cephalaspidea). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 11: 110–133
- Salvini-Plawen, L.v. (1984). Notes on molluscan meiofauna from Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 64: 497–502
- Salvini-Plawen, L.v. (1991). The status of Rhodopidae (Gastropoda: Euthyneura). *Malacologia* 32: 301–311
- Sanders-Esser, B. (1980). Licht und elektron-mikroskopische Untersuchungen zur Bau und Funktionen der Genitalorgane der Ascoglossa (Gastropoda: Euthyneura). PhD Thesis, Wilhelm University, Münster, Germany
- Sanders-Esser, B. (1984). Vergleichende Untersuchungen zur Anatomie und Histologie der vorderen Genitalorgane der Ascoglossa (Gastropoda, Euthyneura). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 111: 195–243
- Sarma, A.L.N. (1975). Three new species of the bivalved gastropods *Julia* and *Berthelinia* found in the eastern Indian Ocean. *Venus* 34: 11–25

16. OPISTHOBRANCHIA

- Sars, G.O. (1878). *Bidrag til Kundskaben om Norges Arktiske Fauna I. Mollusca regionis arcticae Norvegiae*. Christiania Universitets : Christiania 466 pp.
- Schalk, P.H. (1990). Spatial and seasonal variation in pteropods (Mollusca) of Indo-Malayan waters related to watermass distribution. *Marine Biology* 105: 59–71
- Schepman, M.M. (1913). Pulmonata. Opisthobranchia: Tectibranchiata, Tribe Bullomorpha. Pp. 453–494 in Weber, M. & de Beaufort, L.F. (eds) *The Prosobranchia, Pulmonata and Opisthobranchia Tectibranchiata, Tribe Bullomorpha, of the Siboga Expedition*. Monograph 49. *Siboga-Expedition* 32(4)
- Schmekel, L. (1970). Anatomie der genitalorgane von Nudibranchiern (Gastropoda Euthyneura). *Pubblicazioni della Stazione Zoologica di Napoli* 38: 120–217
- Schmekel, L. (1971). Histologie und feinstruktur der genitalorgane von nudibranchiern (Gastropoda, Euthyneura). *Zeitschrift für Morphologie der Tiere* 69: 115–183
- Schmekel, L. (1985). Aspects of evolution within the opisthobranchs. Pp. 221–267 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca. Vol. 10. Evolution*. Academic Press : New York
- Schmekel, L. & Portmann, A. (1982). *Opisthobranchia des Mittelmeeres, Nudibranchia und Saccoglossa. Fauna e Flora del Golfo di Napoli* 40. Springer-Verlag : Heidelberg 410 pp.
- Schmekel, L. & Weischer, M.L. (1973). Die Blutdrüse der Doridoidea (Gastropoda, Opisthobranchia) als ort möglicher hämocyandin-synthese. *Zeitschrift für Morphologie der Tiere* 76: 261–284
- Seager, J.R. (1979). Reproductive biology of the Antarctic opisthobranch *Philine gibba* Strebel. *Journal of Experimental Marine Biology and Ecology* 41: 51–74
- Seager, J.R. (1982). Population dynamics of the Antarctic opisthobranch *Philine gibba* Strebel. *Journal of Experimental Marine Biology and Ecology* 60: 163–179
- Se ed, R. (1976). Observations on the ecology of *Membranipora* (Bryozoa) and a major predator *Doridella steinbergae* (Nudibranchiata) along the fronds of *Laminaria saccharina* at Friday Harbor, Washington. *Journal of Experimental Marine Biology and Ecology* 24: 1–17
- Sentz-Braconnot, E. (1965). Sur la capture des proies par le ptéropode gymnosome *Pneumodermopsis paucidens* (Boas). *Cahiers de Biologie Marine* 6: 191–194
- Sentz-Braconnot, E. & Carré, C. (1966). Sur la biologie du nudibranche pélagique *Cephalopyge trematoides*. Parasitisme sur le Siphonophore *Nanomia bijuga*, nutrition, développement. *Cahiers de Biologie Marine* 7: 31–38
- Sheard, K. (1965). Species groups in the zooplankton of Eastern Australian Slope Waters, 1938–41. *Australian Journal of Marine and Freshwater Research* 16: 219–254
- Shonman, D. & Nybakken, J.W. (1978). Food preferences, food availability and food resource partitioning in two sympatric species of cephalaspidean opisthobranchs. *The Veliger* 21: 120–126
- Short, J.W. & Potter, D.G. (1987). *Shells of Queensland and the Great Barrier Reef. Marine Gastropods*. Robert Brown & Associates : Bathurst, New South Wales vi 135 pp.
- Sleeper, H.L., Paul, V.J. & Fenical, W. (1980). Alarm pheromones from the marine opisthobranch *Navanax inermis*. *Journal of Chemical Ecology* 6: 57–70
- Smallwood, W.M. (1904). The maturation, fertilization, and early cleavage of *Haminea solitaria* (Say.). *Bulletin of the Museum of Comparative Zoology at Harvard College* 45: 259–318
- Smallwood, W.M. (1910). Notes on the hydroids and nudibranchs of Bermuda. *Proceedings of the Zoological Society of London* 1: 137–145
- Smith, B.J., Black, J.H. & Shepherd, S.A. (1989). Molluscan egg masses. Pp. 841–891 in Shepherd, S.A. & Thomas, I.M. (eds) *Marine Invertebrates of Southern Australia. Part II*. South Australian Government Printer : Adelaide
- Smith, E.A. (1891). Descriptions of new species of shells from the 'Challenger' Expedition. *Proceedings of the Zoological Society of London* 1891: 436–445
- Smith, E.A. (1902). Mollusca. Pp. 201–213 in *Report on the Collections of Natural History made in the Antarctic regions during the voyage of the Southern Cross*. British Museum (Natural History) : London
- Smith, S.T. (1967a). The ecology and life history of *Retusa obtusa* (Montagu) (Gastropoda, Opisthobranchia). *Canadian Journal of Zoology* 45: 397–405
- Smith, S.T. (1967b). The development of *Retusa obtusa* (Montagu) (Gastropoda, Opisthobranchia). *Canadian Journal of Zoology* 45: 737–764
- Smith, S.T. & Carefoot, T.H. (1967). Induced maturation of gonads in *Aplysia punctata*. *Nature* 215: 652–653
- Solis, N.B. & von Westernhagen, H. (1978). Vertical distribution of euthecosomatous pteropods in the upper 100 m of the Hilutangan Channel, Cebu, the Philippines. *Marine Biology* 48: 79–87
- Souleyet, F.L.A. (1850). Observations sur les genres *Lophocercus* et *Lobiger*. *Journal de Conchyliologie* 1: 224–238
- Souverbie, S.M. (1861). Descriptions d'espèces nouvelles de l'Archipel Calédonien. *Journal de Conchyliologie* 9: 271–284
- Stebbins, T.D. (1987). Mass mortality of the bubble snail *Bulla gouldiana* Pilsbry, 1893 (Gastropoda: Opisthobranchia). *The Veliger* 30: 95
- Steinberg, J.E. (1956). The pelagic nudibranch, *Cephalopyge trematoides* (Chun, 1889) in New South Wales, with a note on other species in this genus. *Proceedings of the Linnean Society of New South Wales* 81: 184–192
- Stimpson, W. (1855). Descriptions of some new marine invertebrata. *Proceedings of the Academy of Natural Sciences of Philadelphia* 7: 385–395
- Stirts, H.M. & Clark, K.B. (1980). Effects of temperature on products of symbiotic chloroplasts in *Elysia tuca* Marcus (Opisthobranchia: Ascoglossa). *Journal of Experimental Marine Biology and Ecology* 43: 39–47
- Stock, J.H. (1971). *Micrallecto uncinata*, n.gen., n.sp.: a parasitic copepod from a remarkable host, the pteropod, *Pneumodermopsis*. *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 2: 77–79
- Stock, J.H. (1973). *Nannallecto fusii*, n.gen., n.sp.: a copepod parasitic on the pteropod, *Pneumodermopsis*. *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 3: 21–24
- Strenth, N.E. & Blankenship, J.E. (1978). Laboratory culture, metamorphosis and development of *Aplysia brasiliensis* Rang, 1828 (Gastropoda: Opisthobranchia). *The Veliger* 21: 99–103
- Swedmark, B. (1968). The biology of interstitial Mollusca. *Symposia of the Zoological Society of London* 22: 135–149
- Swennen, C. & Dekker, R. (1995). *Corambe batava* Kerbert, 1886 (Gastropoda: Opisthobranchia), an immigrant in the Netherlands, with a revision of the family Corambidae. *Journal of Molluscan Studies* 61: 97–107
- Switzer-Dunlap, M. & Hadfield, M.G. (1977). Observations on development, larval growth and metamorphosis of four species of Aplysiidae (Gastropoda: Opisthobranchia) in laboratory culture. *Journal of Experimental Marine Biology and Ecology* 29: 245–261
- Switzer-Dunlap, M. & Hadfield, M.G. (1979). Reproductive patterns in Hawaiian aplysiid gastropods. Pp. 199–210 in Stancyk, S.E. (ed.) *Reproductive Ecology of Marine Invertebrates*. University of Carolina Press : Columbia, South Carolina
- Taki, I. (1956). *Japonactaeon*, a new genus of Pupidae (Opisthobranchia, Gastropoda). *Bulletin of the National Science Museum* 3: 47–50
- Talavera, P., Murillo, L. & Templado, J. (1987). The genus *Haminoea* Turton & Kingston, 1830 (Opisthobranchia, Bullomorpha) in the southeast of Spain with a description of a new species. *Bolletino Malacologico* 23: 53–68
- Tardy, J. (1970). Contribution à l'étude des métamorphoses chez les nudibranches. *Annales des Sciences Naturelles (Zoologie)* 12: 299–370
- Taylor, D.L. (1968). Chloroplasts as symbiotic organelles in the digestive gland of *Elysia viridis* (Gastropoda: Opisthobranchia). *Journal of the Marine Biological Association of the United Kingdom* 48: 1–15

- Taylor, J.D. (1982). Diets of sublittoral predatory gastropods of Hong Kong. Pp. 907–920 in Morton, B. & Tseng, C.K. (eds) *Proceedings of the First International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, 1980*. Hong Kong University Press : Hong Kong
- Taylor, J.D. (1986). Diets of sand living predatory gastropods at Piti Bay, Guam. *Asian Marine Biology* 3: 47–58
- Tchang, S. (1934). Contribution à l'étude des Opisthobranches de la côte de Tsingtao. *Contributions from the Institute of Zoology, National Academy of Peiping* 2: 1–148
- Tesch, J.J. (1904). The Thecosomata and Gymnosomata of the "Siboga" Expedition. *Siboga Expedition* 16: 1–92
- Tesch, J.J. (1946). The thecosomatous pteropods. I. The Atlantic. *Dana Report* 28: 1–82
- Tesch, J.J. (1948). The thecosomatous pteropods. II. The Indo-Pacific. *Dana Report* 30: 1–45
- Tesch, J.J. (1950). The Gymnosomata. II. *Dana Report* 36: 1–55
- Theide, J. (1975). Shell- and skeleton-producing plankton and nekton in the Eastern North Atlantic Ocean. *Meteor. Forschungs-ergebnisse, Reihe C* 20: 33–79
- Thiele, J. (1912). Die antarktischen Schnecken und Muscheln. *Deutsche Südpolar-Expedition 1901–1903* 13: 183–285
- Thiele, J. (1925). Gastropoda der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition* 21: 158–268
- Thiele, J. (1931). *Handbuch der Systematischen Weichtierkunde*. Gustav Fischer : Jena Vol. 2, Pt 2, pp. 377–778
- Thiriot-Quiévreux, C. (1970). Transformations histologiques lors de la métamorphose chez *Cymbulia peroni* de Blainville (Mollusca: Opisthobranchia). *Zeitschrift für Morphologie der Tiere* 67: 106–117
- Thomas, R.F. (1975). The reproductive system of *Bursatella leachii plei* (Opisthobranchia: Aplysiacea) with special reference to its histology. *Malacologia* 15: 113–131
- Thompson, T.E. (1960a). Defensive acid-secretion in marine gastropods. *Journal of the Marine Biological Association of the United Kingdom* 39: 115–122
- Thompson, T.E. (1960b). Defensive adaptations in opisthobranchs. *Journal of the Marine Biological Association of the United Kingdom* 39: 123–134
- Thompson, T.E. (1967). Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *Journal of the Marine Biological Association of the United Kingdom* 47: 1–22
- Thompson, T.E. (1970). Eastern Australian Pleurobranchomorpha (Gastropoda, Opisthobranchia). *Journal of Zoology, London* 160: 173–198
- Thompson, T.E. (1972a). Observations on *Hexabranhus* from the Australian Great Barrier Reef (Gastropoda: Opisthobranchia). *The Veliger* 15: 1–5
- Thompson, T.E. (1972b). Eastern Australian Dendronotoidea (Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society* 51: 63–77
- Thompson, T.E. (1973a). Euthyneuran and other molluscan spermatozoa. *Malacologia* 14: 167–206
- Thompson, T.E. (1973b). Sacoglossan gastropod molluscs from eastern Australia. *Proceedings of the Malacological Society of London* 40: 239–251
- Thompson, T.E. (1975). Dorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia) (with an appendix by R. Burn). *Journal of Zoology, London* 176: 477–517
- Thompson, T.E. (1976). *Biology of Opisthobranch Molluscs*. Vol. 1. Ray Society : London 207 pp.
- Thompson, T.E. (1979). Biology and relationships of the South African sacoglossan mollusc *Volvatella laguncula*. *Journal of Zoology, London* 189: 339–347
- Thompson, T.E. (1988). Molluscs: benthic opisthobranchs (Mollusca: Gastropoda). *Linnean Society of London, Synopses of the British Fauna (ns)* 8: 1–356
- Thompson, T.E. & Bebbington, A. (1969). Structure and function of the reproductive organs of three species of *Aplysia* (Gastropoda: Opisthobranchia). *Malacologia* 7: 347–380
- Thompson, T.E. & Bennett, I. (1969). *Physalia* nematocysts: utilised by mollusks for defence. *Science* 166: 1532–1533
- Thompson, T.E. & Bennett, I. (1970). Observations on Australian Glaucidae (Mollusca, Opisthobranchia). *Zoological Journal of the Linnean Society* 49: 187–197
- Thompson, T.E. & Brodie, G. (1988). Eastern Mediterranean Opisthobranchia: Runcinidae (Runcinacea), with a review of runcinid classification and a description of a new species from Fiji. *Journal of Molluscan Studies* 54: 339–346
- Thompson, T.E. & Brown, G.H. (1976). British opisthobranch molluscs. Mollusca: Gastropoda. Keys and notes for the identification of the species. *Synopses of the British Fauna, Linnean Society of London (ns)* 8: 1–203
- Thompson, T.E. & Brown, G.H. (1981). Biology and relationships of the nudibranch mollusc *Notobryon wardi* in South Africa, with a review of the Scyllaeidae. *Journal of Zoology, London* 194: 437–444
- Thompson, T.E. & Brown, G.H. (1984). *Biology of Opisthobranch Molluscs*. Vol. 2. Ray Society : London 229 pp.
- Thompson, T.E., Cattaneo, R. & Wong, Y.M. (1990). Eastern Mediterranean Opisthobranchia : Dotidae (Dendronotoidea), Arminidae and Madrellidae (Arminoidea). *Journal of Molluscan Studies* 56: 393–413
- Thompson, T.E. & Colman, J.G. (1984). Histology of acid glands in Pleurobranchomorpha. *Journal of Molluscan Studies* 50: 65–67
- Thompson, T.E., Jarman, G.M. & Zenetos, A. (1985). Infralittoral macrobenthos of the Patias Gulf and Ionian Sea: opisthobranch molluscs. *Journal of Conchology* 32: 71–95
- Thompson, T.E. & Seaward, D.R. (1989). Ecology and taxonomic status of the Aplysiomorph *Akera bullata* in the British Isles. *Journal of Molluscan Studies* 55: 489–496
- Thompson, T.E. & Slinn, D.J. (1959). On the biology of the opisthobranch *Pleurobranchus membranaceus*. *Journal of the Marine Biological Association of the United Kingdom* 38: 507–524
- Todd, C.D. (1979). The population ecology of *Onchidoris bilamellata* (L.) (Gastropoda: Nudibranchia). *Journal of Experimental Marine Biology and Ecology* 41: 213–255
- Todd, C.D. (1981). The ecology of nudibranch molluscs. *Oceanography and Marine Biology, an Annual Review* 19: 141–234
- Todd, C.D. (1983). Reproductive and trophic ecology of nudibranch molluscs. Pp. 225–259 in Russell-Hunter, W.D. (ed.) *The Mollusca*. Vol. 6. Academic Press : London
- Tokioka, T. & Baba, K. (1964). Four new species and a new genus of the family Gastropteridae from Japan (Gastropoda: Opisthobranchia). *Publications of the Seto Marine Biological Laboratory* 12: 201–229
- Troost, D.G. & van der Spoel, S. (1972). Juveniles of *Cavolinia inflexa* (Lesueur, 1813) and *Cavolinia longirostris* (De Blainville, 1821), their discrimination and development (Gastropoda, Pteropoda). *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 2: 221–235
- Tsubokawa, R. & Okutani, T. (1991). Early life history of *Pleurobranchaea japonica* Thiele, 1925 (Opisthobranchia: Notaspidea). *The Veliger* 34: 1–13
- Tsuchida, E. (1991). Rediscovery of *Obrussena moeshimaensis* Habe from off Mishima, Yamaguchi Prefecture. *Chiribotan* 22: 16–18
- Usuki, I. (1966a). The life cycle of *Haloa japonica* (Pilsbry). 1. The larval development. *Science Reports of Niigata University (Series D)* 3: 87–105
- Usuki, I. (1966b). The life cycle of *Haloa japonica* (Pilsbry). II. Spawning and growth. *Science Reports of Niigata University (Series D)* 3: 107–121
- Usuki, I. (1969). The reproduction, development and life history of *Berthellina citrina* (Rüppell & Leuckart) (Gastropoda: Opisthobranchia). *Science Reports of Niigata University, (Series D), Biology* 6: 107–127

16. OPISTHOBRANCHIA

- Usuki, I. (1977). Effects of food algae on the nutrition of *Ercolania boodleae* (Baba), (Opisthobranchia, Gastropoda). *Japanese Journal of Ecology* 27: 103–110
- Vande Vusse, F.J. (1980). A pelagic gastropod first intermediate host for a hemiuroid trematode. *Journal of Parasitology* 66: 167–168
- van der Spoel, S. (1964). Sense organs in *Spongiobranchaea australis* d'Orbigny, 1835 (Gastropoda, Pteropoda). *Beaufortia* 11: 149–159
- van der Spoel, S. (1967). *Euthecosomata, a group with remarkable developmental stages* (Gastropoda, Pteropoda). *Journal van Noorduijn en Zoon. N.V. : Gorinchem* 375 pp.
- van der Spoel, S. (1968). The shell and its shape in Cavoliniidae (Pteropoda, Gastropoda). *Beaufortia* 15: 185–189
- van der Spoel, S. (1972). A taxonomic outline of the Gymnosomata (Mollusca). *Basteria* 36: 75–78
- van der Spoel, S. (1973a). Strobilation in a mollusc; the development of aberrant stages in *Clio pyramidata* Linnaeus, 1767 (Gastropoda, Pteropoda). *Bijdragen tot de Dierkunde* 43: 202–214
- van der Spoel, S. (1973b). Growth, reproduction and vertical migration in *Clio pyramidata* Linné, 1767 forma *lanceolata* (Lesueur, 1813), with notes on some other Cavoliniidae (Mollusca, Pteropoda). *Beaufortia* 21: 117–134
- van der Spoel, S. (1974). Geographical variation in *Cavolinia tridentata* (Mollusca, Pteropoda). *Bijdragen tot de Dierkunde* 44: 100–112
- van der Spoel, S. (1976). *Pseudothecosomata, Gymnosomata and Heteropoda* (Gastropoda). Bohn, Scheltema, and Holkema : Utrecht 484 pp.
- van der Spoel, S. (1979). Strobilation in a pteropod (Gastropoda, Opisthobranchia). *Malacologia* 18: 27–30
- van der Spoel, S. (1985). Note on the taxonomy of the family Notobranchaeidae and description of *Notobranchaea bleekerae* n. sp., a species new to science (Gastropoda, Pteropoda). *Basteria* 49: 29–36
- van der Spoel, S. (1987). *Diacavolinia* nov. gen. separated from *Cavolinia* (Pteropoda, Gastropoda). *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 11: 77–79
- van der Spoel, S. & Diester-Haass, L. (1976). First records of fossil gymnosomatous protoconchae. *Bulletin Zoologisch Museum, Universiteit van Amsterdam* 5: 85–88
- van der Spoel, S. & Heyman, R.P. (1983). *A Comparative Atlas of Zooplankton. Biological Patterns in the Oceans*. Springer-Verlag : Berlin 186 pp.
- van der Spoel, S. & Newman, L. (1990). Juveniles of the pteropod *Hyalocylis striata* (Gastropoda, Pteropoda). *Basteria* 54: 203–210
- van der Spoel, S. & Pafort-van Iersel, T. (1985). Notes on the taxonomy of the family Notobranchaeidae and description of *Notobranchaea bleekerae* n. sp., a species new to science (Gastropoda, Pteropoda). *Basteria* 49: 29–36
- Vaught, K.C. (1989). *A Classification of the Living Mollusca*. American Malacologists : Florida 189 pp. Edited by Abbott, R.T. & Boss, K.J.
- Vayssière, A. (1880). Recherches anatomiques sur les mollusques de la famille des Bullidés. *Annales des Sciences Naturelles (Zoologie)* (6) 9: 1–123
- Vayssière, A. (1883). Recherches anatomiques sur les genres *Pelta* et *Tylodina*. *Annales des Sciences Naturelles (Zoologie)* (6) 15: 1–46
- Vayssière, A. (1885). Recherches zoologiques et anatomiques sur les Mollusques opisthobranches du Golfe de Marseille. Première partie, Tectibranches. *Annales du Muséum d'Histoire Naturelle de Marseille, Zoologie* 2(3): 1–181
- Vayssière, A. (1898). Monographie de la famille des Pleurobranchidés. *Annales des Sciences Naturelles (Zoologie)* 8: 209–402
- Vayssière, A. (1901). Monographie de la famille des Pleurobranchidés. (Deuxième et dernière partie). *Annales des Sciences Naturelles (Zoologie)* 8: 1–85
- Vayssière, A. (1902). Opisthobranches. In *Expéditions scientifiques du "Travailleur" et du "Talisman" pendant les années 1880–1883*. Ministère de l'Instruction publique : Paris pp. 221–280 pls 9–11
- Vayssière, A. (1903). Recherches zoologiques et anatomiques sur les mollusques opisthobranches du Golfe de Marseille. *Annales du Muséum d'Histoire Naturelle de Marseille, Zoologie, Supplémentaire* 8: 69–108
- Vayssière, A. (1906a). Recherches zoologiques et anatomiques sur les Opisthobranches de la Mer Rouge et du Golfe d'Aden. Part 1: Les Tectibranches. *Annales de la Faculté des Sciences de Marseille* 16: 19–90
- Vayssière, A. (1906b). Mollusques nudibranches et marséniadés. Pp. 1–51 in Joubin, L. (Professor au Muséum d'Histoire Naturelle) *Expédition Antarctique Française (1903–1905). Commandée par le Dr Jean Charcot, Sciences Naturelles, Documents Scientifiques*. Masson et Cie : Paris
- Vayssière, A. (1917). Recherches zoologiques et anatomiques sur les mollusques amphieures et gastropodes (opisthobranches et prosobranches). Pp. 1–44 in *Deuxième Expédition Antarctique Française 1908–1910*. Masson et Cie : Paris
- Vélain, C. (1877). Description des mollusques. Passage de Venus sur le soliel (Décembre 1874). Expedition française aux Îles Saint-Paul et Amsterdam. *Zoologie. Archives de Zoologie expérimentale et générale* 6: 98–144
- Verco, J.C. (1909). Notes on South Australian Marine Mollusca, with descriptions of new species. Part X. *Transactions and Proceedings and Report of the Royal Society of South Australia* 33: 270–276
- Veron, J.E.N. (1986). *Corals of Australia and the Indo-Pacific*. Angus & Robertson : North Ryde 644 pp.
- Vincente, N. & Arnaud, P.M. (1974). Invertébrés marins des XIIème et XVème Expéditions antarctiques françaises en Terra Adélie, 12, Gastéropodes opisthobranches. *Tethys* 5: 531–548
- Vine, P. (1986). *Red Sea Invertebrates*. Immel Publishing : London 224 pp.
- Vitalis, T.Z., Spence, M.J. & Carefoot, T.H. (1988). The possible role of gut bacteria in nutrition and growth of the sea hare *Aplysia*. *The Veliger* 30: 333–341
- Wägele, H. (1985). The anatomy and histology of *Phyllidia pulitzi* Pruvot-Fol, 1962, with remarks on the three Mediterranean species of *Phyllidia* (Nudibranchia: Doridacea). *The Veliger* 28: 63–79
- Wägele, H. (1988). Riesenwuchs contra spektakuläre Farbenpracht – Nudibranchia der Antarktis. *Natur und Museum* 118: 46–53
- Wägele, H. (1990a). Opisthobranchia (Hinterkiemer). Pp. 72–77 in Seig, J. & Wägele, J.W. (eds) *Fauna der Antarktis*. Paul Parey : Berlin & Hamburg
- Wägele, H. (1990b). Revision of the genus *Austrodoris* Odhner, 1926 (Gastropoda, Opisthobranchia). *Journal of Molluscan Studies* 56: 163–180
- Wägele, H. (1991). Studies on the morphology and anatomy of the Antarctic nudibranch genera *Pseudotrionia* Thiele, 1912 and *Telarma* Odhner, 1934 with a discussion of the family Charcotiidae Odhner, 1926 (Nudibranchia : Opisthobranchia). *Zoological Journal of the Linnean Society* 101: 359–389
- Wägele, H., Barnes, D.K., & Bullough, L.W. (1995) Redescription of *Charcotia granulosa* Vayssière, 1906 (Nudibranchia: Arminoidea: Charcotiidae) from Signy Island, Antarctica. *Journal of Molluscan Studies* 61: 197–207
- Wägele, H., Bullough, L.W. & Barnes, D.K. (1995). Anatomy of *Pseudotrionia* Thiele, 1912 and *Notaeolidia* Eliot, 1905 (Gastropoda: Opisthobranchia: Nudibranchia) from Signy Island, Antarctica. *Journal of Molluscan Studies* 61: 209–213
- Wägele, H. & Hain, S. (1991). Description of a new notaspidean genus and species (Opisthobranchia: Notaspidea) from the Antarctic Ocean. *Journal of Molluscan Studies, Supplement, T.E. Thompson Memorial Issue* 57(4): 229–242
- Warén, A. (1989). New and little known Mollusca from Iceland. *Sarsia* 74: 1–28
- Warmke, G.L. & Almodovar, L.R. (1972). Observations on the life cycle and regeneration in *Oxynoe antillarum* Mörch, an ascoglossan opisthobranch from the Caribbean. *Bulletin of Marine Science* 22: 67–74

- Watson, R.B. (1878). Sur l'animal du *Ringicula auriculata*. *Journal de Conchyliologie* 26: 312–313
- Wagh, G.R. & Clark, K.B. (1986). Seasonal and geographic variation in chlorophyll level in *Elysia tuca* (Ascoglossa: Opisthobranchia). *Marine Biology* 92: 483–487
- Wawra, E. (1974). The rediscovery of *Strubellia paradoxa* (Strubell) (Gastropoda, Euthyneura, Acochlidacea) on the Solomon Islands. *The Veliger* 17: 8–10
- Wawra, E. (1979). Zur systematischen Stellung von *Platyhedyle denudata* Salvini-Plawen, 1973 (Opisthobranchia, Gastropoda). *Zeitschrift für Zoologische Systematik und Evolutionforschung* 17: 221–225
- Wawra, E. (1980). *Acochlidium bayerfehlmanni* spec. nov. (Gastropoda: Opisthobranchia: Acochlidacea) from Palau Islands. *The Veliger* 22: 215–218
- Wawra, E. (1988). Beitrag zur Kenntniss des Zentralnervensystems von *Platyhedyle denudata* Salvini-Plawen 1973 (Ascoglossa, Gastropoda). *Annalen des Naturhistorischen Museums in Wien, Botanik und Zoologie* 90B: 401–406
- Wawra, E. (1989). Zur Kenntnis der interstitiellen Opisthobranchierart *Hedylopsis spiculifera* (Kowalevsky) (Mollusca, Gastropoda). *Zoologica Scripta* 18: 397–403
- Wawra, E. (1991). Beitrag Zur Kenntniss des Genitaltrakts von *Platyhedyle denudata* Salvini-Plawen 1973 (Mollusca: Gastropoda: Ascoglossa). *Annalen des Naturhistorischen Museums in Wien, Botanik und Zoologie* 92B: 269–275
- Wells, F.E. (1976). A preliminary examination of euthecosomatous pteropods off the central coast of Western Australia. *Records of the Western Australian Museum* 4: 327–334
- Wells, F.E. (1978). Distribution of thecosomatous pteropods off the central coast of Western Australia. *Australian Journal of Marine and Freshwater Research* 29: 853–858
- Wells, F.E. (1983). First record of the euthecosomatous pteropod, *Limacina helicoides* Jeffreys, 1877 from the Indian Ocean. *Journal of the Malacological Society of Australia* 6: 89–90
- Wells, F.E. (1984). *A Guide to the Common Molluscs of South-western Australian Estuaries*. Western Australian Museum : Perth 112 pp.
- Wells, F.E. (1986). A redescription of the sea hare *Aplysia gigantea* Sowerby, 1869. *Journal of the Malacological Society of Australia* 7: 173–178
- Wells, F.E. & Bryce, C.W. (1986). *Seashells of Western Australia*. Western Australian Museum : Perth 207 pp.
- Wells, F.E., Bryce, C.W., Clarke, J.E. & Hansen, G.M. (1990). *Christmas Shells. The marine molluscs of Christmas Island (Indian Ocean)*. Christmas Island Natural History Association : Christmas Island 99 pp.
- West, H.H., Harrigan, J.F. & Pierce, S.K. (1984). Hybridization of two populations of a marine opisthobranch with different developmental patterns. *The Veliger* 26: 199–206
- White, A.W. (1977). Dinoflagellate toxins as a probable cause of an Atlantic herring (*Clupea harengus harengus*) kill, and pteropods as apparent vectors. *Journal of the Fisheries Research Board of Canada* 34: 2421–2424
- Willan, R.C. (1976). The opisthobranch *Thecacera pennigera* (Montagu) in New Zealand, with a discussion of the genus. *The Veliger* 18: 347–352
- Willan, R.C. (1978a). The nomenclature of three Pacific *Bulla* species. *Journal of the Malacological Society of Australia* 4: 57–68
- Willan, R.C. (1978b). An evaluation of the notaspidean genera *Pleurobranchopsis* Verrill and *Gymnotoplax* Pilsbry (Opisthobranchia: Pleurobranchinae). *Journal of Conchology* 29: 337–344
- Willan, R.C. (1979a). The ecology of two New Zealand opisthobranch molluscs. PhD Thesis, University of Auckland, Auckland
- Willan, R.C. (1979b). New Zealand locality records for the aeolid nudibranch *Fiona pinnata* (Eschscholtz). *Tane* 25: 141–147
- Willan, R.C. (1981a). Rediscovery of *Runcinella zelandica* Odhner, 1924 (Opisthobranchia: Runcinacea). *National Museum of New Zealand Records* 2: 5–8
- Willan, R.C. (1981b). A new abyssal arminacean nudibranch from New Zealand. *New Zealand Journal of Zoology* 8: 325–330
- Willan, R.C. (1983). New Zealand side-gilled sea slugs (Opisthobranchia: Notaspidea: Pleurobranchidae). *Malacologia* 23: 221–270
- Willan, R.C. (1984a). A review of diets in the Notaspidea (Mollusca: Opisthobranchia). *Journal of the Malacological Society of Australia* 6: 125–142
- Willan, R.C. (1984b). The Pleurobranchidae (Opisthobranchia: Notaspidea) of the Marshall Islands, central-west Pacific Ocean. *The Veliger* 27: 37–53
- Willan, R.C. (1987a). Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. *American Malacological Bulletin* 5: 215–241
- Willan, R.C. (1987b). Phylogenetic systematics and zoogeography of Australian nudibranchs. 1. Presence of the aeolid *Godiva quadricolor* (Barnard) in Western Australia. *Journal of the Malacological Society of Australia* 8: 71–85
- Willan, R.C. (1988). The taxonomy of two host-specific, cryptic dendronotoid nudibranch species (Mollusca: Gastropoda) from Australia including a new species description. *Zoological Journal of the Linnean Society* 94: 39–63
- Willan, R.C. (1989). First record of the nudibranch *Trapania brunnea* in New Zealand waters with comments on intraspecific variation in the species. *The Veliger* 32: 182–184
- Willan, R.C. & Coleman, N. (1984). *Nudibranchs of Australasia*. Australasian Marine Photographic Index : Caringbah, New South Wales 56 pp.
- Willan, R.C. & Morton, J.E. (1984). *Marine Molluscs. Part 2. Opisthobranchia*. Leigh Marine Laboratory, University of Auckland : Auckland 106 pp.
- Williams, G.C. & Gosliner, T.M. (1979). Two new species of nudibranchiate molluscs from the west coast of North America, with a revision of the family Cuthonidae. *Zoological Journal of the Linnean Society* 67: 203–223
- Wimpenny, R.S. (1966). *The Plankton of the Sea*. Faber & Faber Ltd : London 235 pp.
- Wisely, B. (1962). An outline of the development of the bivalve gastropod *Midorigai australis* Burn, 1960. *Journal of the Malacological Society of Australia* 1(6): 37–39
- Wormelle, R.L. (1962). A survey of the standing crop of plankton of the Florida current. VI. A study of the distribution of the pteropods of the Florida current. *Bulletin of Marine Science of the Gulf and Caribbean* 12: 95–136
- Wormuth, J.H. (1985). The role of cold-core Gulf Stream rings in the temporal and spatial patterns of euthecosomatous pteropods. *Deep-Sea Research* 32: 773–788
- Yamasu, T. (1968). Anatomy and histology of a bivalved gastropod, *Julia japonica*. *Biological Journal of Okayama University* 14: 35–53
- Yonge, C.M. & Thompson, T.E. (1976). *Living Marine Molluscs*. Collins : London 288 pp.
- Yonow, N. (1989). Feeding observations on *Acteon tornatilis* (Linnaeus) (Opisthobranchia: Acteonidae). *Journal of Molluscan Studies* 55: 97–102
- Yoshioka, P.M. (1982). Predator-induced polymorphism in the bryozoan *Membranipora membranacea* (L.). *Journal of Experimental Marine Biology and Ecology* 61: 233–242
- Young, D.K. (1969). *Okadaia elegans*, a tube-boring nudibranch mollusc from the central and west Pacific. *American Zoologist* 9: 903–907
- Zilch, A. (1959–1960). Gastropoda, Teil 2, Euthyneura. In Schindewolf O.H. (ed.) *Handbuch der Paläozoologie*. Vol. 6. Gebroder Bornträger : Berlin xii, 834 pp.

PULMONATA

— CHAPTER 17 —

DEFINITION AND GENERAL DESCRIPTION

The Pulmonata is one of the three subclasses into which the class Gastropoda has been subdivided: the other two are the Prosobranchia and the Opisthobranchia. Pulmonates are molluscs that use a lung as the respiratory surface. The name Pulmonata is used here to describe this group of gastropods without necessarily retaining the taxonomic meaning of the grouping. Pulmonates were the subject of a two volume treatise some years ago, well introduced by Fretter (1975). The group can be divided into three major subunits, the orders Systellommatophora, Basommatophora and Eupulmonata (Fig. 17.1); the last consists mainly of the suborder Stylommatophora plus a few minor groups. The Pulmonata is now considered to be a polyphyletic grouping (Solem 1978a; Haszprunar & Huber 1990; Bieler 1992).

Pulmonates are essentially land and freshwater molluscs, but representatives of a few genera, recognised as amongst the most primitive, live intertidally. Land and freshwater groups also occur among some prosobranch groups (some neritopsines and caenogastropods), however, there are no terrestrial opisthobranchs and only one or two opisthobranch species might be termed freshwater taxa. The characters differentiating pulmonates from other gastropods are largely associated with the change from marine to non-marine habitats. The comparatively benign marine environment provides an osmotically stable medium for reproduction, respiration, feeding and body support, in contrast to freshwater and terrestrial habitats. Rather than invoking a serial aquatic route for terrestrial invasion from salt to freshwater, then to land, it is now thought that most pulmonates were derived from marine taxa via salt marsh to terrestrial forms. The present day freshwater fauna thus represents a secondary invasion of the aquatic environment. This better explains similarities in the general organisation of the Basommatophora and Stylommatophora, as well as their mutual differences from other gastropods.

Pulmonates have the general gastropod body form of head, foot and visceral mass. The basic arrangement of the mantle cavity and the digestive and reproductive systems is shown in Figure 17.2. A spirally coiled shell is usually present though it may be limpet-shaped, reduced, wholly enveloped in the mantle, or lost totally. An operculum is lacking in adults except in the Amphibolidae and Glacidorbidae. The mantle cavity lacks a ctenidium, but secondary gills or pseudobranchs may be developed in some marine and freshwater forms. The opening to the mantle cavity is reduced, by fusion of the mantle border with the neck, to a narrow, contractile opening forming a respiratory pore or pneumostome on the right side of the animal. The internal dorsal wall of the mantle cavity is highly vascularised, permitting respiratory exchange. This arrangement is often referred to as a 'lung' or the pulmonary cavity. The kidney opens into the pulmonary cavity via a simple papilla in primitive forms whereas in more advanced forms it voids via a ureter terminating near the pneumostome. Ordinarily the anus is also situated near the pneumostome.

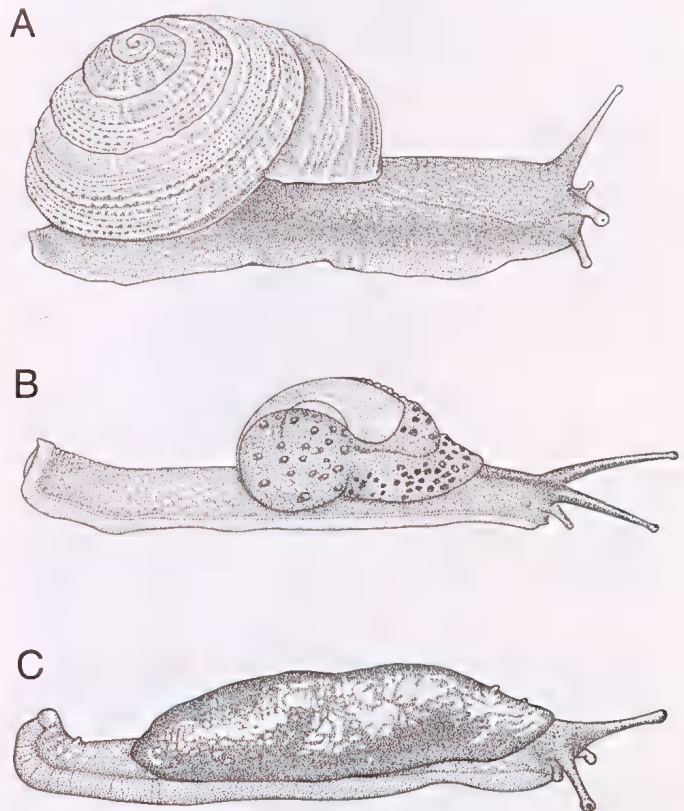


Figure 17.1 Representative eupulmonatan pulmonates. A, *Angolypta launcestonensis* (Caryodidae), found in the litter of wet forests in north-eastern Tasmania. B, *Fastosarion aquila* (Helicarionidae), a semi-slug from the wet forests of coastal northern New South Wales and south-eastern Queensland: note the mantle lobes over the shell. C, *Cystopelta* sp., from Mt Superbus in south-eastern Queensland, one of a small number of slugs of the endemic family Cystopeltidae. mal, mantle lobe; sh, shell. (A, after photograph by R.C. Kershaw; B, C, after photographs by Queensland Museum) [C. Eadie]

The buccal mass bears a single, dorsal jaw consisting of fine rods or platelets, except in some carnivorous forms in which the jaw has been lost. The radula is usually oblong, typically with straight rows of many small teeth, although this varies greatly, particularly in carnivorous forms. The nervous system is usually euthyneurous, and shows a shortening of the visceral portions and the formation of a circumoesophageal ring composed of five ganglia. The structure of the nervous system and its significance in elucidating the phylogeny of the pulmonates are discussed by Van Mol (1967), Haszprunar (1988), Tillier (1989) and Haszprunar & Huber (1990).

Pulmonates are usually simultaneous hermaphrodites with various levels of fusion of the male and female ducts. Fertilisation is internal and for this a variety of ancillary copulatory structures have developed. Specialised glandular structures are also present to form the egg and facilitate the passage, transfer and receipt of sperm, which are often contained in a spermatophore. Most groups are oviparous and have complex egg formation, including

17. PULMONATA

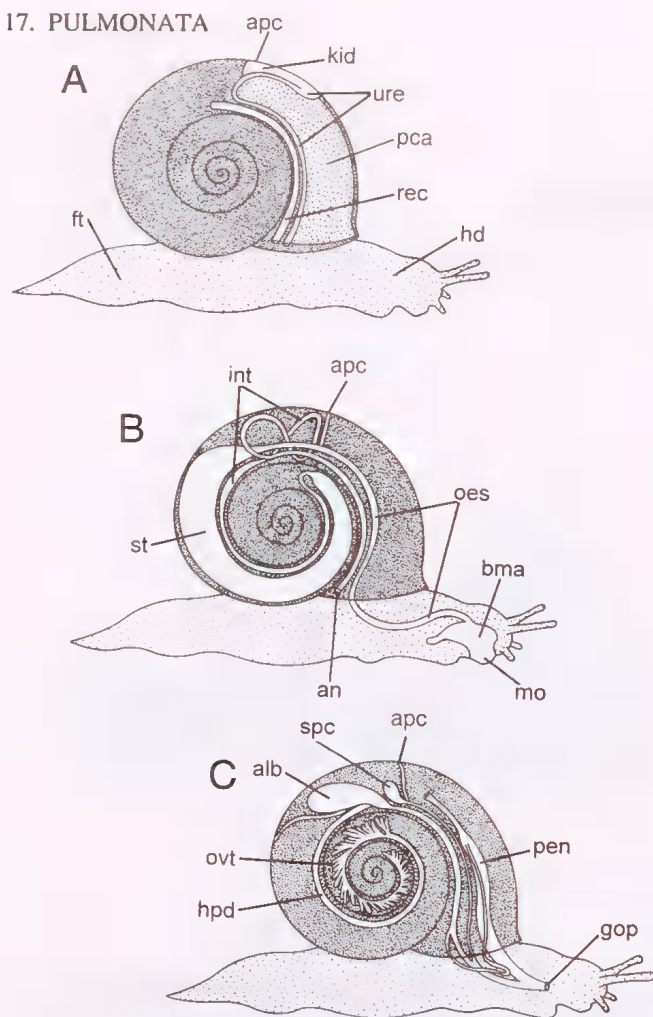


Figure 17.2 Arrangement of basic pulmonate organ systems. A, location and extent of the pallial cavity and associated organs. B, location of the digestive tract; the digestive gland which occupies most of the area above the stomach has been omitted. C, location of the genital tract. Organs above the apex of the pallial cavity (apc) are termed 'apical genitalia', those below are 'pallial genitalia'. alb, albumen gland; an, anus; apc, apex of pallial cavity; bma, buccal mass; ft, foot; gop, gonopore; hd, head; hpd, hermaphroditic duct; int, intestine; kid, kidney; mo, mouth; oes, oesophagus; ovt, ovotestis; pca, pallial cavity; pen, penis; rec, rectum; spc, spermatheca; st, stomach; ure, ureter. (After Solem 1974)

[C. Eadie]

impervious, calcareous shelled eggs in many terrestrial forms. Several groups exhibit ovoviviparity and some members of the Glacidorbidae have been described as viviparous.

The Australian pulmonate fauna consists of 44 families containing about 750 described native and over 40 introduced species (Smith 1992). Thirteen families are represented in the Australian fauna only by recently introduced species, many of which are serious pests. Many of these were well established before 1850. It is thought that only 50% of the total fauna has so far been described; the remainder, awaiting description, is mainly from northern and eastern Australia (Stanisic 1994b). A great many groups are in need of modern revisions and large areas of the continent have never been examined systematically for pulmonates. Though the research collections in the various State museums are large and are expanding, for many species preserved animals are unavailable for anatomical studies.

HISTORY OF DISCOVERY

Between 1770 and 1990 more than 1500 species names were erected for Australian pulmonates (including Lord Howe and Norfolk Islands). Many of these have now been relegated to synonymy by later revisions. The number of pulmonate species with their type locality in Australia (including Lord Howe and Norfolk Islands) described between 1770 and 1990 provides an insight into the pattern of discovery of the Australian pulmonates (1770–1799, 1; 1800–1849, 88; 1850–1899, 726; 1900–1949, 613; 1950–1990, 145).

These periods reflect the four main phases into which the discovery and description of Australia's pulmonate fauna can be subdivided, although these phases are not really chronological and there is a great deal of overlap in time. These are: voyages of exploration; collection for European specialists; studies by early Australian workers; research in State museums and by State specialists, and the work of the American researcher, Alan Solem.

Almost all the species described before 1850 were collected on voyages of discovery and exploration. Consequently, they were collected near or on the coastal fringe, usually near a good anchorage in a bay or inlet and were usually either large, spectacular and/or very abundant, as the collectors were not trained malacologists. With a few exceptions they were also only seen by the describers as dead shells with no information on the animal or habitat. In fact in many instances even the locality given was only a general one (Kershaw 1987a).

Cook's voyages to Australia appear to have yielded no pulmonate specimens that were described, although some may have been collected and described later and their source not recorded. In sharp contrast to this, on several of the early French voyages of exploration, many specimens were collected and transported promptly to Paris for description either by the collectors or by the leading natural historians of the day, such as Lamarck, Férussac and others. The naturalists who collected material on these voyages included Péron and Lesueur (*Le Géographe*, 1800–1802), Quoy and Gaimard (*Uranie*, 1817; *l'Astrolabe*, 1826–1829), Lesson (*La Coquille*, 1822) and Hombron and Jacquinot (*l'Astrolabe* and *Le Zélée*, 1837–1840). These voyages yielded over 50 new Australian pulmonate species, mainly from southern Australia. By comparison, in terms of the pulmonates collected, the only British voyage of importance was that of the HMS *Rattlesnake* (1847–1848), on which MacGillivray collected material from northern Australia. More details of these voyages are given by Dance (1986). Hardly any of the early inland explorers collected snails.

As the continent became better known and more settled, some of the early pioneers were either interested enough to collect snails for their own sake, for example, George French Angas, or were employed to collect specimens by dealers based in Europe. Perhaps the best known of all the dealers was Hugh Cuming who employed several snail collectors in Australia including Cunningham, Strange and MacGillivray. Specimens thus collected were sent back to Europe where they were made available to various experts for description; many were figured in the large illustrated monographs produced at the time.

Several of the more prominent workers who described many Australian pulmonates in the mid-nineteenth Century were H. Pfeiffer, A. Adams, and L.A. Reeve, and several of the Sowerby family. Placement of type specimens of the newly described species in European museums was characteristic of this period, even though, with the discovery of gold, many of the well-established, richer colonies had their own natural history museums, quite capable of being safe repositories for the primary reference material of this 'new' fauna.

The era of collectors soon gave way to, and overlapped with, the era of the early Australian pulmonate researchers. These resident malacologists started publishing their findings, and lodged their reference material in Australia. The founder and dominant personality of this era was undoubtedly Dr J.C. Cox, who first published a catalogue of Australian land shells (Cox 1864) and then his illustrated *Monograph of Australian Land Shells* (Cox 1868). A complete description of Cox's contribution is given by Richardson (1970). Cox encouraged people like Legrand to continue to document the fauna, and influenced regional workers like Petterd, besides establishing a foundation for the era of the professional malacologists such as Brazier, Hedley, Iredale and Cotton.

Very soon after the various State museums were established, regional studies of the pulmonate fauna were initiated. From about 1870 to the 1930s, many parts of Australia were covered by regional reports and local lists by such workers as Petterd, Johnston, Tate and Gabriel. These culminated in the publication of basic lists of the land and freshwater Mollusca of Australia by Iredale (1937a, 1937b, 1938, 1943a). These lists formed a watershed in pulmonate taxonomic studies in Australia and provided a springboard for the modern studies by Kershaw, Smith, Solem, Stanisic, and others.

MORPHOLOGY AND PHYSIOLOGY

External Features

The external features of pulmonates are of primary importance in their identification and reflect their way of life as well as the relationships of the species. External features can be categorised under two main headings: those concerned with the shell and those to do with the soft anatomy of the body of the animal.

Shell

Possession of a helicoid coiled shell is probably the primitive condition of both basommatophoran and stylommatophoran pulmonates. This shell would have had a large last whorl into which the animal could withdraw its whole body. In common with other groups of molluscs, the shell consists of an outer layer or periostracum made of the complex organic material 'conchin' (similar to arthropod chitin) and several layers of crystalline calcareous material. The periostracum may contribute much of the shell sculpture and colour patterning.

Modifications to the basic shell form occur across groups of pulmonates. Ten of the 44 pulmonate families that occur in Australia, have some or all members with the shell absent, or so reduced that the animal can no longer withdraw into it, or internal and reduced to a fragile remnant or a few calcareous fragments. Animals in which the shell is either lost or remains internal are called slugs. Those in which the shell is greatly reduced are considered to represent a trend towards the slug-like form and have been called 'semi-slugs' by Solem (1974).

Three distinct characteristics of pulmonate shells have significance in the identification of families, genera and species within the group. These are shape and form; sculpture of both the protoconch and teleoconch; and colour pattern.

Pulmonate shells can vary in shape from high-spined to globose to planispiral. In one planorbid genus, *Ancylastrum*, the spire is reduced to a vestigial spiral on a large limpet-like shell, whereas three families, the Siphonariidae, Trimusculidae and Ancyliidae, have virtually lost all trace of coiling to become entirely limpet-shaped. The presence or absence of an umbilicus in helicoid shells and its diameter compared to the diameter of the shell are important taxonomic features, as are the size of the last whorl compared to the rest of the shell, the size and shape of the aperture and whether the aperture is protected by 'teeth', lamellae or other barriers. Several families are characterised by the type of apertural 'teeth' they possess and their precise location around the aperture. Finally the thickness of the shell can give an indication of the environmental variation experienced by the animal. Most freshwater groups have comparatively thin shells with few calcareous elements, perhaps reflecting availability of calcium. Carnivorous species, of Rhytididae and Zonitidae, also show a reduction in calcareous shell elements giving a much lighter more flexible shell, possibly related to the carnivorous habit. On the other hand many groups have thick, solid shells which provide effective protection from many forms of predation and desiccation. The Amphibolidae and Glacidorbidae are the only pulmonate families with a horny operculum. This is an unusual feature in pulmonate snails, but is typically seen in other shelled gastropods.

All species of shelled pulmonates show lines on their shells corresponding to discontinuities in shell growth throughout their lives. Some of the many forms of shell sculpture are shown in Figure 17.3. Also many species have thickened ridges, mainly in the periostracum, giving the shell a regular sculpture. This can take the form of simple radial or spiral ridges or lines or can be a complex mixture of primary ribs with secondary riblets or a reticulate pattern of fine lines (Fig. 17.3). Sculpture can also take the form of an irregular rugose pattern or even granulations and a mat of fine hairs or spines. The sculpture found on the embryonic shell (protoconch) can be totally different from that found on the adult shell (teleoconch) and this too can be an indicator of relationships among species, or useful in distinguishing taxa.

The colours, and the nature and intensity of the colour pattern are of major importance in identification. These are largely features of the periostracum. Shells can have a variety of background colours, mainly white, cream, yellow and shades of brown in Australia, although the shells of some tropical pulmonates can be bright green or red. Superimposed on this background colour is a variety of regular bands, either a darker or lighter variant of the ground colour, a contrasting colour or a series of blotches or flames. In some forms, the colour and patterning are constant and constitute a species-specific character, whereas in others, the patterning is variable and sometimes may be related to specific habitat preferences of morphs. The patterning can be so variable that a shell with a normally cream background colour can be almost black in appearance due to the broadening of dark brown bands to cover the entire shell. Also, within pulmonate species, shell size and shape often exhibit extreme variation, with some recurrent environmental correlations (Goodfriend 1986).

Body of the Animal

After the shell, the external features of the body of the animal are the next most accessible characters for the family and generic placement of any pulmonate specimen. External characters can be considered under four main headings. These are: shape, form and colour; mantle and pneumostome; features of the head; and features of the tail.

The general shape of the body can be important. Members of the Rhytididae are adapted for carnivory. The shell is carried far back on the animal almost over the tail (Fig. 17.51A). The anterior part of the body is greatly elongated to accommodate the much enlarged buccal mass (Fig. 17.8B; Solem 1974), more normally short as in Figure 17.8A. In the native slug family Cystopeltidae, unlike any other slug family, the visceral mass is separated from the foot posteriorly, and is carried more like the visceral mass of a snail (Fig. 17.1C). Body colour and pattern are also important, particularly in slugs, many of which show cryptic colouration. In contrast, two colour forms of a species in the Athoracophoridae have a bright orange or red body colour. The possibility that this is a warning colour needs experimental verification.

The shape and position of the mantle are very important taxonomic characters, particularly in slugs, as are the position of the pneumostome and the presence of mantle appendages. The mantle covers and encloses the mantle cavity (pulmonary cavity), which in most pulmonates is the principal site of respiration. It is usually at the front of the visceral hump and creates a space into which the animal can withdraw its head-foot complex. The pneumostome usually opens on the right mantle margin. The mantle is reduced to a small triangular area in the mid-dorsal region in the Athoracophoridae, from which short trachea-like tubes carry air to the major organs; in the Testacellidae, it is situated at the posterior end of the body, under the vestigial shell. The mantle and mantle cavity are absent in the slugs belonging to the Onchidiidae, Rathouisidae and Veronicellidae. Several families have characteristic mantle appendages. The Physidae, a group of sinistral freshwater snails introduced into Australia, is characterised by digitate mantle processes (Fig. 17.35B). Large mantle lappets are present in some helicarionids. These fleshy lobes extend over the reduced shell of some species and provide protection and camouflage (Fig. 17.1B).

17. PULMONATA

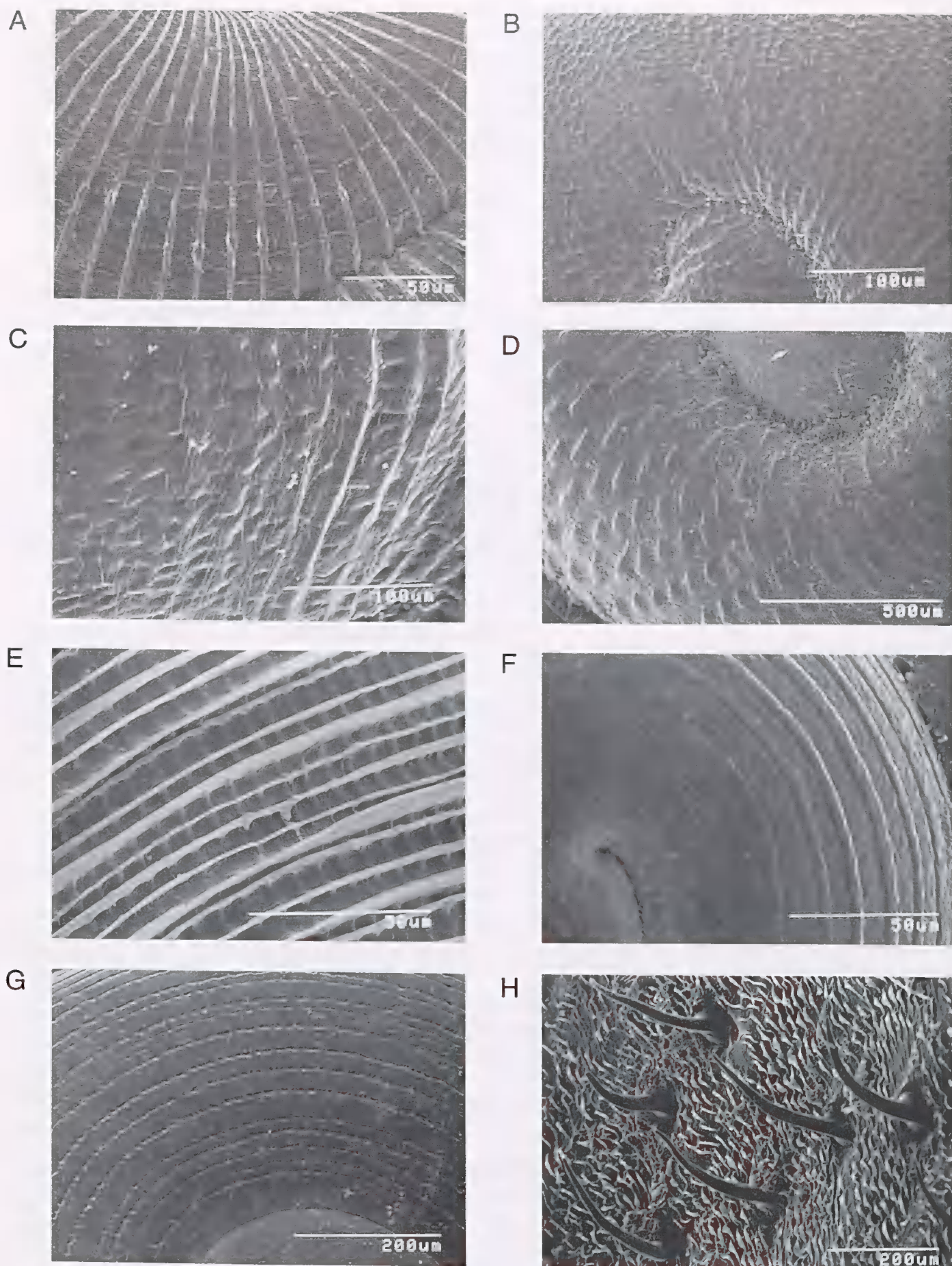


Figure 17.3 Pulmonate shell sculpture. A, prominent radial ribs and weak spiral cordlets on the protoconch of *Discocharopa aperta* (Charopidae). B, minute punctations on the protoconch of *Papisoma circumlitum* (Pupillidae). C, malleate sculpture on the body whorl of *Cylindroverrilla hedleyi* (Pupillidae). D, elongate pustules on the protoconch of *Oreomava otwayensis* (Charopidae). E, reticulate sculpture on the body whorl of *Lotula microcosmos* (Punctidae). F, spiral cords on the protoconch of *Nitor medioximus* (Helicariionidae). G, notched incised spiral grooves on the protoconch of *Austrochloritis porteri* (Camaenidae). H, periostracal setae on the body whorl of *Austrochloritis porteri* (Camaenidae).

[Queensland Museum]

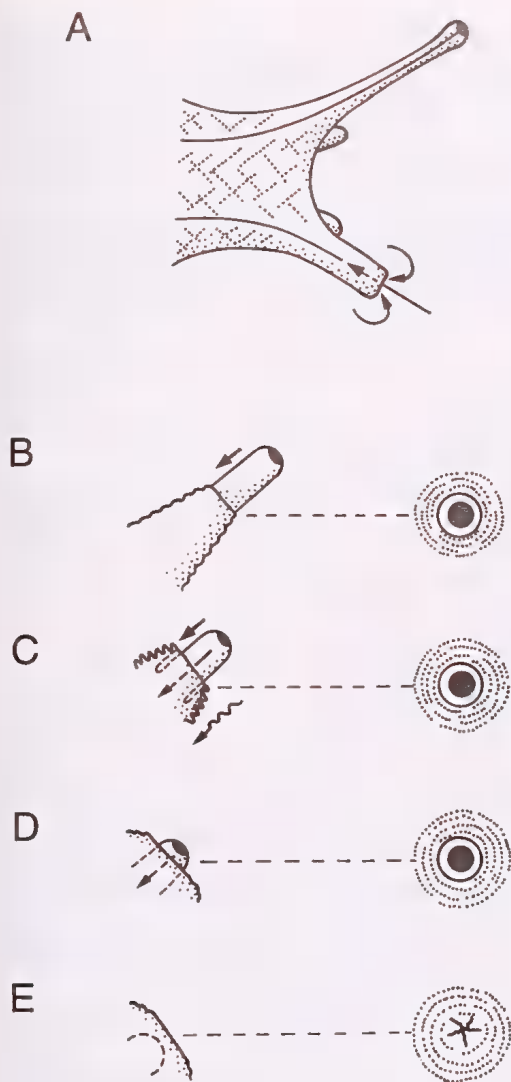


Figure 17.4 Retraction of the optic tentacles in pulmonates. A, stylomatophoran with introversible tentacles. B–E, progressive tentacle retraction in the Athoracophoridae – corresponding lateral and dorsal views. The proximal portion of the tentacle contracts while the distal eyestalk is withdrawn (not introverted) into the snail's anterior body. (After Burch 1968) [C. Eadie]

Systellomatophorans and basomatophorans usually have one pair of tentacles (absent in species of *Smeagol*) whereas stylomatophorans typically have two pairs (Fig. 1.61C). Eyes are situated at the base of the tentacles in basomatophorans, at the tip of each longer, superior tentacle in stylomatophorans (Fig. 17.4A) and the tip of the only tentacles in the Onchidiidae, Rathouisiidae and Veronicellidae. The family Athoracophoridae is unique amongst pulmonates in that the optic tentacles retract rather than invert (Fig. 17.4B–E; Burch 1968). The other external feature associated with the head is the genital pore which typically opens on the right side of the head about half way between the optic tentacle and the pneumostome.

The posterior end of the foot varies in shape from hemispherical in section to triangular when the tail bears a mid-dorsal keel. In a few families, particularly the Arionidae, Helicarionidae and Charopidae, a prominent caudal gland on the tip of the tail produces extra mucus associated with locomotion, feeding or reproductive activity.

Musculature and Locomotion

The mechanism and functions of the hydrostatic skeleton found in pulmonates are outlined under Circulation.

The gross anatomy of the musculature of the head-foot region described in outline here is based largely on an account of the musculature of *Helix pomatia* by Trappman (1916). The foot is highly muscular and contains longitudinal, transverse and dorso-ventral fibres, and muscles inclined at various angles to these three directions, as well as circular muscles around the head-foot (Fig. 1.13C). Most of these muscles insert on different parts of the body wall at both ends. The space between the muscle fibres of the foot is filled with blood as part of the haemocoel. The anterior half of the foot is served with bundles of retractor muscles which are convergent with the columellar muscle. The head is also served with retractor muscles which converge with the columellar muscle, including a buccal retractor muscle and four tentacular retractor muscles (Fig. 17.5). The single penial retractor muscle originates on the dorsal body wall. The body wall of the head and foot is highly muscular with longitudinal, circular and oblique muscle fibres. Attached to the body wall near the mouth are several discrete muscles concerned with the operation of the buccal mass. The highly muscular floor of the mantle cavity contributes to breathing and the protrusion of the head-foot from the shell. A slug has very similar musculature to that of *Helix*, except that the retractor muscles insert on the body wall in the vicinity of the vestigial shell. The primary function of the retractor muscle system is the withdrawal of the head-foot complex into the shell, a detailed sequence for which is given by Jones (1975) and Emberton (1989).

Pulmonates are primarily adapted for locomotion over hard substrata. The foot is a muscular organ with a large sole upon which the animal crawls and remains attached to the substratum, using the adhesive properties of mucus. During locomotion a continuous trail of mucus is laid down from the supra-pedal mucous gland at the anterior end, and the sole passes over this using either cilia on the sole or waves of muscular contraction. Most pulmonates move by utilising both the ciliary and muscular functions of the pedal sole. Aquatic species and some small terrestrial species use mainly cilia, and larger terrestrial species use muscular waves.

Two main types of muscular waves are seen in pulmonates. Direct pedal waves which move in the same direction as the animal and retrograde pedal waves which move in the opposite direction to the animal. Both wave types may traverse the foot as a single or monotaxic system of waves or they may pass along the foot as two systems of waves, one each side of the mid-line, a condition termed ditaxic. Ditaxic waves may be alternate or opposite. A third arrangement found occasionally has four separate systems of waves, termed tetrataxic. Almost all pulmonates using muscular pedal waves for locomotion use direct, monotaxic waves.

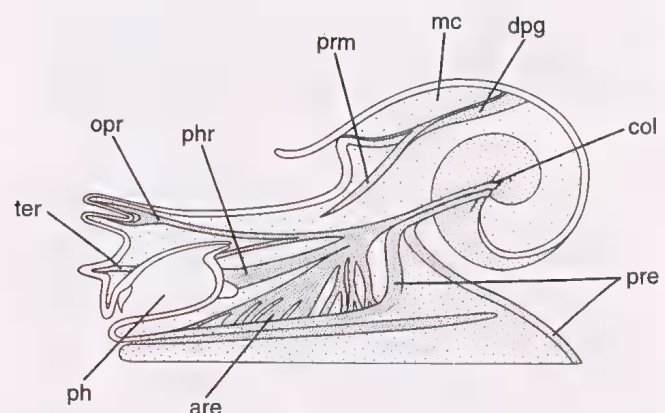


Figure 17.5 The retractor muscle system of a typical snail genus, *Helix*. are, anterior retractor muscle; col, columella; dpg, diaphragm; mc, mantle cavity; opr, optic retractor muscle; ph, pharynx; phr, pharyngeal retractor muscle; pre, posterior retractor muscle; prm, penial retractor; ter, tentacular retractor muscle. (After Solem 1974, modified from Trappman 1916)

[C. Eadie]

17. PULMONATA

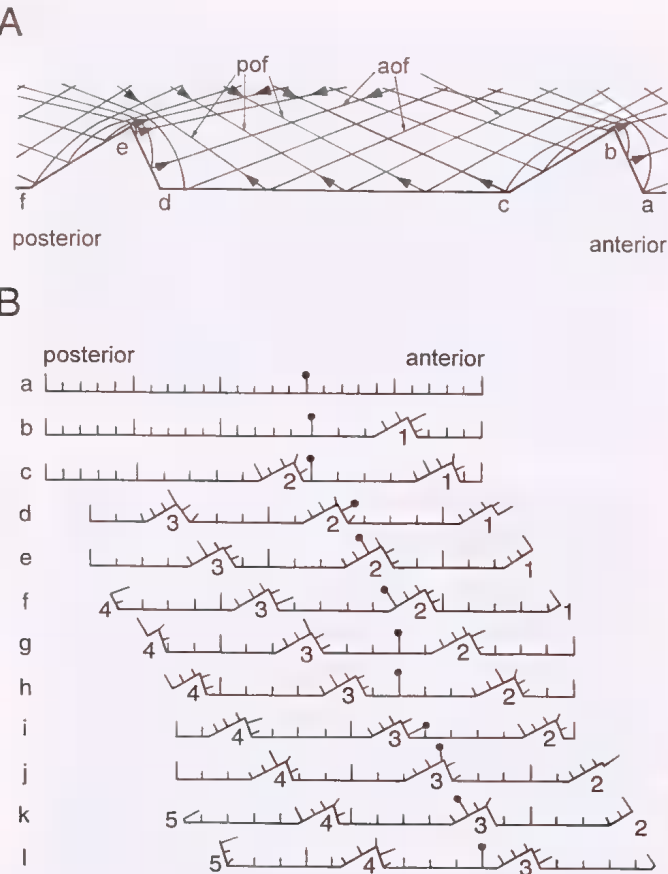


Figure 17.6 Methods of locomotion in pulmonates. **A**, *Agriolimax* sp. (Limacidae), contracting muscle fibres bear large arrow heads; the posterior oblique fibres (pof) contract between waves (c–d) pulling the body of the slug forward and exerting backward thrust on the substratum; the anterior oblique fibres (aof) contract to pull the epithelium of the sole forwards and to form each pedal wave (a–b–c and d–e–f). **B**, an animal such as a slug which uses direct locomotory waves; a hypothetical diagram to illustrate the commencement of locomotion. Vertical lines represent arbitrary division of foot into sectors with every fifth being highlighted and one marked with a dot to emphasise direction of uplift. (After Jones 1973) [C. Eadie]

In the Onchidiidae, a family of primitive pulmonates, only one monotaxic direct wave passes along the sole at a time. In all other pulmonates using direct monotaxic waves, more than one wave is seen at a time on the sole during locomotion. Two or three waves at a time are seen on the sole in the two small introduced species *Oxychilus alliarius* and *Cionella lubrica*. In the large introduced slug, *Limax maximus*, 11 to 19 waves may be present on the sole at any one time.

The musculature of the foot has a very distinct arrangement. Immediately ventral to the supra-pedal mucous gland lies a layer of longitudinal muscle fibres. A relatively unrestricted haemocoelic space lies between this muscular layer and the more ventral epithelium of the sole. This space is crossed by two sets of oblique longitudinal muscle fibres, continuous at their dorsal end with the longitudinal fibres and attached at their ventral end to the epithelium of the sole. One set (the anterior oblique fibres) applies an anteriorly directed upward force to the epithelium, whereas the other (the posterior oblique fibres) applies a posteriorly directed upward force to the epithelium (Fig. 17.6). The forces exerted at the dorsal end of each set are in the opposite direction to those exerted at the epithelial ends.

This system is thought to function in locomotion as follows. The anterior oblique fibres contract and lift the epithelium upwards and forwards relative to both the body and the substratum, producing a wave. As the region of contraction of the fibres continues forwards, each fibre then relaxes and the epithelium is re-applied to the substratum. Once the epithelium is back on the substratum it adheres to the mucous trail and becomes stationary. The posterior fibres then contract, thus moving forward the layer

of longitudinal muscle and the body of the animal above it, since the epithelial end of each fibre is stationary on the substratum. This movement restores the anterior fibres to their original length. Another pedal wave follows, again moving the sole forward by contraction of the anterior fibres and restores the posterior fibres to their original length. Thus the two sets of fibres are mutually antagonistic (Jones 1973).

In a few species, a form of more rapid muscular locomotion does not involve successive muscular waves. This locomotion is called 'looping' or 'galloping' and involves a forward progression by flexing and extending the whole of the head-foot region.

Ciliary locomotion is used by almost all basommatophorans, many of the smaller stylommatophorans and, to some extent, by juveniles of the larger pulmonates. The critical factor seems to be the effective weight of the animal in the medium in which it lives (Jones 1973). The pulmonate foot is covered with cilia. Locomotion is achieved by the beating of the cilia in the mucus under the sole, propelling the body along. The two important factors are length of cilia and frequency of the beat. Very few detailed studies have been carried out to describe the exact functioning and control mechanisms of this form of locomotion.

Feeding and Digestion

Very little is known about the anatomy and physiology of feeding and digestion in any native Australian pulmonate. This section is based on an excellent review of the pulmonate alimentary canal by Runham (1975). This in turn is based largely on studies on *Lymnaea stagnalis* by Carriker (1946) and others, and *Agriolimax (= Deroceras) reticulatus* by Walker (1969) and others. Both these species have been introduced into Australia. Pulmonate alimentary systems conform to a general pattern (Figs 17.2B, 17.7). The mouth leads into the buccal mass (Fig. 17.8), a complex muscular structure containing the radula and the jaw, where food receives the secretions from the salivary glands. Food is then passed via the oesophagus and ancillary structures of crop and gizzard to the stomach, which also receives ducts from the large and complex digestive gland. After most of the digestion and food absorption has taken place, the residue is then passed down the intestine where faeces are formed to be passed out via the rectum and anus.

The structures used for feeding form the buccal mass. This is a globular organ at the front of the head that consists of the radula, jaw, odontophore 'cartilage' and associated muscles. No true cartilage is found in any heterobranch (Haszprunar 1985). The buccal cavity is continuous with the mouth anteriorly, via the oral

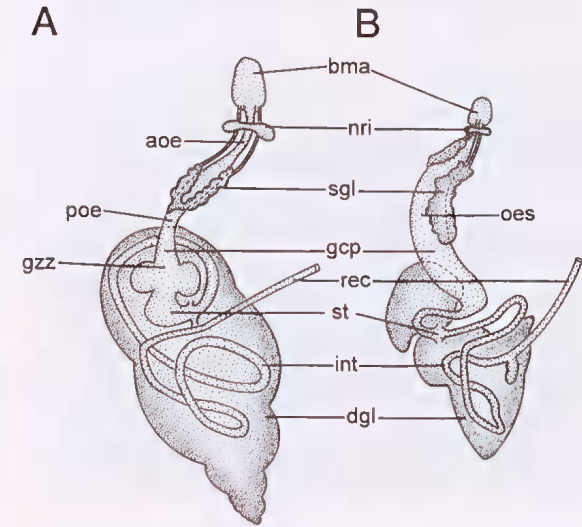


Figure 17.7 Pulmonate digestive systems. **A**, *Lymnaea stagnalis* (Lymnaeidae), a basommatophoran. **B**, *Deroceras reticulatum* (Limacidae), a stylommatophoran. aoe, anterior oesophagus; bma, buccal mass; dgl, digestive gland; gcp, gastric crop; gzz, gizzard; int, intestine; nri, nerve ring; oes, oesophagus; poe, posterior oesophagus; rec, rectum; sgl, salivary gland; st, stomach. (After Runham 1975) [C. Eadie]

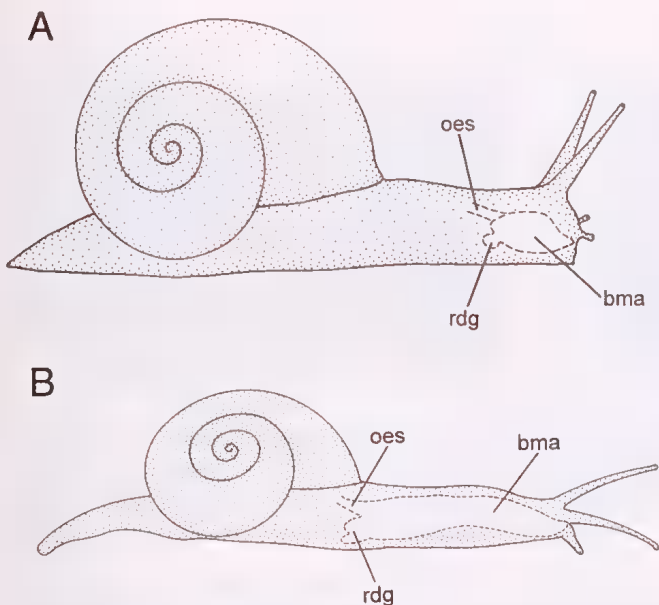


Figure 17.8 The pulmonate buccal mass varies in size according to feeding habit. **A**, *Helix* sp. (Helicidae), a herbivore; the buccal mass is short. **B**, *Strangesta* sp. (Rhytididae), a carnivore; the buccal mass is greatly enlarged as a modification for carnivory. bma, buccal mass; oes, oesophagus; rdg, radular gland. [C. Eadie]

tube, and with the oesophagus postero-dorsally. The mouth is surrounded by a series of sensory lips with associated mucous glands. At the anterior end of the buccal cavity part of the cuticle is thickened by chitin to form the single, dorsal jaw. The jaw varies in structure from group to group and is absent in specialised carnivorous groups. Dorsally, posterior to the jaw, a groove – the dorsal food channel – leads directly back into the oesophagus. This groove is bounded laterally by a narrow band of ciliated epithelium and numerous mucous glands.

Bulging into the buccal cavity from its floor is the large movable odontophore. This consists of the so-called odontophore ‘cartilage’, muscles and the radula which covers most of its surface (Fig. 17.9). The odontophore contains many muscle fibres and vesicular connective tissue cells which are fluid-filled and may act as a hydrostatic skeleton. The radula consists of a highly flexible membrane to which hard teeth are attached in rows. The size, shape and form of the teeth usually vary across a transverse row. In many species it is easy to distinguish a central tooth and fields of lateral and marginal teeth, whereas in others these intergrade. The various forms and numbers of teeth can be used in identification, and radula formulae can be defined for taxa; the formula for *Helix aspersa* is 45–50.20.1.20.45–50, and indicates a central tooth with 20 lateral teeth and 45–50 marginal teeth on each side. Teeth in any longitudinal row are more or less identical in size and shape. The radula is secreted at its posterior end by the radular gland. This gland is folded up to form a tubular structure such that its lateral edges nearly meet dorsally. A rod of connective tissue, the collostyle, fills the centre of this tube. At the posterior tip of the gland are specialised cells, the odontoblasts, that secrete much of the radula. Details of the mechanism of secretion and formation of the teeth are given by Runham (1963, 1975). The action of the radula in feeding (Fig. 17.9) has been described for *Lymnaea stagnalis* by Hubendick (1957) and for several slug species by Runham & Hunter (1970). The backward-pointing teeth can either be used as a rasp to crop the surface film of algae from a hard substratum (Fig. 17.10A), to ‘bite’ off pieces of a solid plant food (Fig. 17.10C) or to hold and to ingest large whole prey in carnivorous forms (Fig. 17.10B).

The salivary glands consist of many sacs of cells (acini), from which small collecting ducts merge to form the large, paired salivary ducts that empty into the postero-dorsal part of the buccal cavity. The glands produce an amylase together with small amounts of trypsin-like protease, and mucus (Evans & Jones

1962). The saliva provides lubrication during feeding, assists with the removal of food from the radula and initiates extracellular digestion (Runham & Hunter 1970).

Food is passed back from the buccal cavity into the oesophagus, which broadens out in many species into a holding sac or crop (Fig. 17.7B). In most stylommatophorans the crop is filled with a reddish brown liquid known as crop juice. This contains a rich soup of enzymes which are active against a wide range of polymers, such as carbohydrates, proteins and lipids (Runham & Hunter 1970). These enzymes are derived largely from the digestive gland which empties into the stomach and it is thought that during periods of inactivity the juice is passed forward from the stomach into the crop where it is held in readiness for the next period of feeding activity. Food is held in the crop for up to several hours, during which extensive extracellular digestion takes place (Walker 1969).

The crop leads directly into the stomach, a sac with various ciliary tracts and grooves forming transport pathways. Ducts carrying enzymes from the digestive gland open into it and from it the food passes into the intestine. *Lymnaea stagnalis* has a large, highly muscular gizzard, which normally contains sand grains (Fig. 17.7A; Carriker 1946). A caecum is also present and has a sorting area leading to the two digestive gland openings. In most stylommatophorans both gizzard and sorting area are absent and the stomach is largely an area of food transport and exchange with no trituration function (Fig. 17.7B). The variation in the structure of the gastric region within the different superfamilies of pulmonates is described by Tillier (1989). In particular he describes the differences associated with carnivory where the digestive tract is shorter and simplified compared to the herbivorous groups. The differences in digestive tract morphology associated with the process of limacisation are described by Tillier (1984a).

Suitable fine particles and soluble materials are passed from the stomach into the digestive glands (Walker 1969) by muscular pulsations of the stomach and digestive gland. Larger particles are excluded by ciliated folds. Waste material from the stomach and from the digestive gland is passed, via grooves in the walls of the stomach and digestive gland ducts, to the intestinal groove.

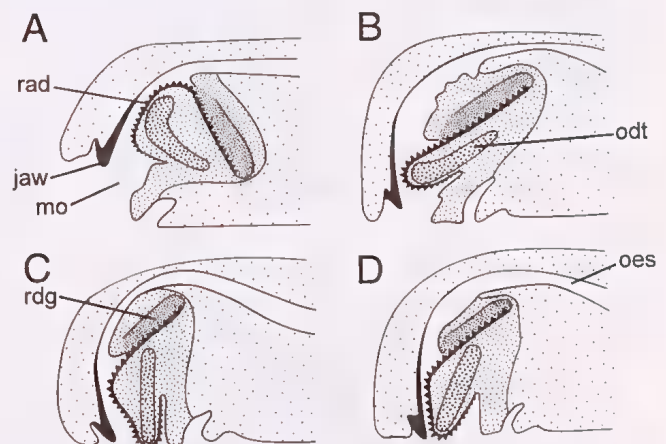


Figure 17.9 Sagittal sections through the buccal mass of *Lymnaea stagnalis* (Lymnaeidae) showing the movements during the feeding cycle. **A**, resting phase; the mouth is closed, the jaw retracted into the buccal cavity and the odontophore has an almost vertical position. **B**, phase 1: the buccal mass is rotated, the mouth is opened and the median jaw moves anteriorly and downwards; the odontophore also rotates, and the odontophore cartilage is pulled into a horizontal or forward tilting position and then is moved forward and pressed towards the mouth; contraction of the cartilage muscles straightens the cartilage and makes it rigid; the radula is stretched tight over the surface of the cartilage. **C**, phase 2: the vertically held odontophore is protracted through the mouth against the substratum and is ready for its feeding stroke. **D**, phase 3: the tip of the odontophore now in contact with the substratum moves forward and the forwardly directed teeth on the outside of the odontophore are dragged through the food material; as the odontophore moves forwards the median jaw is pulled back and held against the radula at the end of the feeding stroke; the mouth begins to close. jaw, jaw; mo, mouth; odt, odontophore cartilage; oes, oesophagus; rad, radula; rdg, radular gland. (After Runham 1975) [C. Eadie]



Figure 17.10 Pulmonate radulae from different feeding groups. A, *Cystopelta petterdi* (Cystopeltidae), central section of radula showing the many very small, fine teeth; this species probably feeds on bacteria or microalgae. B, *Austrorhytida capillacea* (Rhytididae), several tooth rows across the radula showing the lanceolate teeth grading in size to a large dagger-like tooth towards the outside of each side; this species is an active predator, feeding on other snails and slugs. C, *Stenacapha hamiltoni* (Charopidae), section of radula showing the variation in shape between the central (top right) and lateral teeth; this species probably feeds on microfungi.

[A, A. Daniell; B, C, B.J. Smith]

The digestive gland is the largest organ in the pulmonate body and is composed of a series of branching ducts ending in complex, blind tubules into which the gland cells empty. The main functions of the gland are absorption of food materials at various stages in its digestion, the secretion of enzymes, storage of reserve materials and excretion. Very small particles (less than $0.01\ \mu\text{m}$) enter the gland and are passed into the cells for intracellular digestion. The range of enzymes produced by the gland (Runham 1975) includes cellulase and chitinase. These two unusual enzymes are found in very few animals; their action is mainly extracellular in the lumen of the crop and stomach.

Undigested and waste particulate material is passed via ciliary pathways at the start of the intestine, where it is consolidated and mixed with further mucus to form fairly solid faeces for defecation. Passage of material along the intestine is comparatively slow, taking about seven hours in *Agriolimax* (= *Deroceras*) (Walker 1972). Strong intracellular enzymes are present in the epithelial cells but these are not secreted into the lumen of the tract. The long stay of material in the intestine may allow further time for the cellulase and chitinase, in particular, to act, and absorption of further digestive products takes place in the intestine followed by further intracellular digestion. Faeces are then passed through the rectum and expelled via the anus.

Most of these studies have been carried out on species of the Limacidae, Arionidae and Helicidae (Runham & Hunter 1970). Much more work needs to be carried out on these processes in

other groups of pulmonates, since the few species that have been studied in detail have shown many significant differences from one another, and all are higher stylommatophorans. Studies, particularly of Australian endemic families and lower pulmonates, may bring to light major new observations.

Circulation

The pulmonate heart is a simple, two chambered (ventricle and auricle), muscular organ situated just in the roof of the pulmonary cavity (17.11). All venous blood eventually reaches the venous circle along the edge of the pulmonary cavity and around the pneumostome. Pulmonary arteries then conduct the blood to the capillary network in the lung roof where it is oxygenated. The capillaries link with pulmonary veins which drain into a main pulmonary vein. This vessel conveys the blood to the auricle of the heart. It then passes to the ventricle which pumps the blood via the anterior and posterior aortae into beds of capillaries associated with various organs. Here the vessels end in ostioles which are surrounded by a dense network of muscle fibres capable of occluding the opening and so regulating the flow of blood into the haemocoel. The presence of septa within the haemocoel allows differential pressures to be built up. The transverse septum separates the visceral haemocoel from the cephalopodal haemocoel, and other septa occur at different places in the anterior haemocoel (Fretter 1975). Kisker (1923) described two horizontal septa in *Helix pomatia* with ostia controlled by muscle fibres. The more dorsal of these leads forward from close to the anterior end of the transverse septum beneath the thick layer of connective tissue of the neck and head, enclosing a space exclusively for blood. Anteriorly, before it inserts on the head, it fuses with the second septum which crosses the haemocoel to isolate the buccal mass and anterior oesophagus from the reproductive ducts lying above them.

Retraction of the head-foot into the shell is achieved by contraction of the various retractor muscles attached to the columellar muscle. During this sequence air is expelled from the pulmonary cavity and some blood is redistributed to allow room for the head-foot to be housed within the shell. Retraction and protrusion of the head have been investigated by Sommerville (1973) and Dale (1974). Unlike retraction, protrusion takes place in a number of steps or cycles and is not continuous.

The haemocoel of many pulmonates is thought to act as hydrostatic skeleton. It provides for antagonism of musculature, support of the shell and visceral organs, and erection of the tentacles (Dale 1973; Jones 1975). Aquatic forms tend to have the musculature of the body wall less well developed than terrestrial pulmonates (Plesch, Janse & Boer 1975). This is thought to reflect the greater hydrostatic pressure required to support the body of land-based forms.

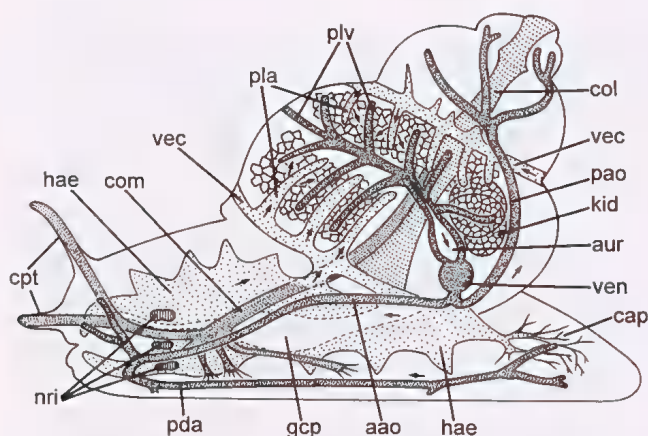


Figure 17.11 Circulatory system and haemocoelic spaces of *Helix pomatia* (Helicidae). aao, anterior aorta; aur, auricle; cap, capillaries; col, columella; com, columellar muscle; cpt, cephalic tentacle; gcp, gastric crop; hae, haemocoel; kid, kidney; nri, nerve ring; pao, posterior aorta; pda, pedal artery; pla, pulmonary arteries; plv, pulmonary veins; vec, venous circle; ven, ventricle. (After Borrodaile et al. 1958)

[C. Eadie]

Phase 1 of protrusion starts when the pneumostome is opened and the foot is pushed slowly outwards. The diaphragm contracts downwards, forcing blood into the head and sucking air into the pulmonary cavity (Dale 1974). In phase 2, the diaphragm is raised to its resting position, the pneumostome is closed and a pressure develops within the pulmonary cavity which forces air into the most posterior part of the cavity. The foot ceases protruding and retracts slightly which may cause a high pressure in the cephalic sinus and push the diaphragm upwards. Phases 1 and 2 are alternated six or seven times to effect full protrusion. For the head to evaginate there must be a redistribution of blood within the haemocoel and blood is shifted from the sub-renal sinus and visceral sinus into the head. Dale (1974) has shown that heart rate and ventricular systolic pressure increase during protrusion, but the venous return pressure does not. Thus the heart increases its output to pump up the head by a redistribution of the aortic blood through constriction of the visceral artery. The disposition of other internal organs during retraction and extension has been investigated in Australian land snails by Emberton (1989).

Excretion

Pulmonates are soft bodied animals which contain considerable amounts of water. They have colonised both marine and freshwater habitats and many have been particularly successful in terrestrial environments including harsh desert conditions. Problems associated with water loss (land snails) and water accumulation (freshwater species) have led to the enhanced development of the ureter. The ureter (Fig. 17.2A) is involved in water and ion resorption, and has been developed as a specialisation of the kidney. The ureter may be a simple tubular structure as in basommatophorans or, as in stylommatophorans, a complex arrangement involving a primary and ectodermal secondary ureter which has arisen as an adaptation to terrestrial life (Andrews 1988).

Pulmonates have a single renal organ or kidney which is a coelomoduct characterised by deeply folded walls. It is usually located posteriorly in the roof of the mantle cavity and is linked to the pericardial sac through a renopericardial pore (Fig. 17.2A). In freshwater pulmonates the hydrostatic pressure of the blood in the heart results in the continuous transfusion of a clear filtrate into the pericardium and subsequently into the kidney where it is mixed with nitrogenous waste from the lining cells of the kidney. The final composition of the urine is determined by a combination of renal secretion, ionic resorption in the kidney and water resorption in the ureter. In terrestrial pulmonates the filtration is direct, from the renal capillaries into the kidney. The renopericardial aperture is small and little if any fluid is lost from the pericardium to the kidney.

The structure and shape of the excretory organs (kidney and ureter) of pulmonates are highly variable. Delhay & Bouillon (1972a, 1972b, 1972c) compared the excretory organs of various Basommatophora and examined their evolutionary and adaptive significance. The most primitive basommatophorans, the shore-dwelling Ellobiidae and Otinidae, have a simple kidney with

no ureter. The marine siphonariids have a simple, large sac-like kidney (Hubendick 1978). In primitive limnic Basommatophora, the kidney may be divided into a proximal saccular region and a distal tubular portion (nephridial pouch) which contains the ureteric pore. This anterior tubular extension of the kidney is involved in osmoregulation. In the higher limnic Basommatophora, for example, Planorbidae, a ureter has developed (Delhay & Bouillon 1972a) and the kidney shape correlates with changes in the shape of the mantle cavity. In sinistral Planorbidae, the kidney forms a loop at the left side of the last whorl and the ureter is a short, reflexed, anterior termination of the nephridial pouch. In the Ancyliidae, the ureter is very long and loops backwards and forwards before it gives rise to a posterior renal opening.

The extent of osmoregulation in the Basommatophora varies. In the marine intertidal species of *Siphonaria* the body fluid is normally isotonic with seawater (Machin 1975). They have little ability to regulate their haemolymph concentration but can tolerate a wide range of external concentrations. This is important in an environment where seawater can be either diluted by rain or concentrated by the sun. Behaviourally, *Siphonaria* species cope with extremes in external media concentration by exclusion, by clamping the limpet-like shell tightly to the substratum.

The freshwater pulmonates face a somewhat different problem. They have a much lower body fluid concentration than marine species but are still hypertonic with respect to the outside environment and are subject to a continuous osmotic inflow of water through the body wall. The problem is overcome by producing an almost continuous flow of urine to 'bale' themselves out, and by hyperosmotic regulation through the active uptake of inorganic ions, for example, sodium and chloride, at the body surface (Andrews 1988). Water is not voided solely by the kidney and the production of 'wet' faeces and associated mucus are two further means of eliminating water from the body.

In both marine and freshwater pulmonates, water currents produced by cilia sweep the excretory products from the mantle cavity.

Among the Systellommatophora, the marine Onchidiidae have a typical renal pouch that opens through a long renal papilla into a diverticulum of the mantle cavity. In the terrestrial Rathouisiidae and Veronicellidae, the papilla is replaced by an elongate ureter which has similar histological features to the ureter of stylommatophorans (Delhay & Bouillon 1972c). The ureter in the Veronicellidae is a straight tube which opens at the posterior end of the body, adjacent to the anus.

Land pulmonates, in contrast to freshwater groups, are primarily concerned with water conservation. Although equipped with a basic pre-adaptation to life on land (the shell), desiccation is an ongoing problem (Table 17.1). There is no free flow of water from the kidney and the excretory product consists almost entirely of insoluble uric acid (see Fig. 1.64A). White crystalline deposits accumulate in the kidney and are discharged at intervals (Andrews 1988). Pallial water or a 'squirt' of excreted water must be used occasionally to flush the products through the pneumostome.

Table 17.1 Loss of water through the shell in terrestrial pulmonate snails (based on weight loss of distilled water through empty shells with the aperture sealed). (From Machin 1975)

Species	Temperature (°C)	Relative humidity (%)	Shell loss (mg/g body wt/h)	% of total inactive loss	Authority
<i>Arianta arbustorum</i>	26	45	0.0139	2.3	Cameron 1970a
<i>Cepaea hortensis</i>	26	45	0.0084	2.2	Cameron 1970a
<i>Cepaea nemoralis</i>	26	45	0.0059	1.8	Cameron 1970a
<i>Helix aspersa</i>	22	70	0.0079	4.6	Machin 1967
<i>Otala lactea</i>	22	70	0.017	25.8	Machin 1967
<i>Sinumelon remissum</i>	20	dry air	0.014	70.0	Warburg 1965
<i>Sphincterochila boissieri</i>	22	70	0.0086	61.5	Machin 1967

17. PULMONATA

Table 17.2. Oxygen consumption (Q_{O_2}) of some pulmonates. (After Ghiretti & Ghiretti-Magaldi 1975)

Species	Q_{O_2} $\mu\text{l O}_2/\text{g wet wt/h}$	Temperature ($^{\circ}\text{C}$)
<i>Cepaea hortensis</i>	80	15
<i>Cepaea vindobonensis</i> (summer)	125	20
<i>Cepaea vindobonensis</i> (winter)	51	20
<i>Helicigona lapicida</i>	96	15
<i>Agriolimax agrestis</i>	194	23
<i>Helicella obvia</i>	180	23
<i>Helix pomatia</i>	20–80	15
<i>Lymnaea stagnalis</i>	11	-

The main sites of resorption in stylommatophorans are the primary and secondary ureters, with conditions favouring resorption in the distal parts (Andrews 1988). The primary ureter resorbs water and salts creating a urine hypotonic to the haemolymph. The secondary ureter then resorbs additional water. The final composition of excretory products has been found to vary in stylommatophoran slugs and snails. In the European slug *Agriolimax reticulatum*, less than 1.5% of nitrogenous waste is lost as gaseous ammonia and 92% as uric acid and xanthine. In active snails, gaseous ammonia constitutes 5% of the waste products and rises to 30% in hibernating snails (Andrews 1988).

Among stylommatophoran ureters, there are several different structural patterns, correlated with the progressive evolution of land snails (Solem 1976, 1978a). Some of these patterns have been used to define major subgroupings.

The orthurethran ureter differs significantly from that of the Sigmurethra and resembles that of the Basommatophora in that the ureter is a secondary specialisation of the kidney and is not clearly separated from it. The ureter lacks ciliated cells and ends in a retrograde groove (Delhay & Bouillon 1972b). The ureteric pore is some distance from the pneumostome and pallial water is needed to flush out the excretory products. In a few taxa (some Enidae), a pseudosigmurethrous condition has developed in which a series of rectal and renal folds form a structurally closed sigmoid 'ureter' which opens at the pneumostome (Fig. 17.12).

The sigmurethran ureter begins at the anterior tip of the kidney and reflexes posteriorly along its margin before reflexing anteriorly along the hindgut to the pneumostome. The reflexed portion of the ureter (secondary ureter) may be an open groove (most Holopodopes) or a closed, heavily vascularised tube. A further variation is seen in the 'mesurethran' kidney which lacks an anterior extension and has the ureteric pore as a simple opening at the kidney tip. An open, reflected, ciliated excretory groove runs to the pneumostome (Delhay & Bouillon 1972b). Some authors consider this development to define an additional subgrouping – the Mesurethra. In slugs, the ureter and kidney configurations are often highly modified to accommodate the spatial requirements of visceral hump reduction. An incomplete secondary ureter has been recorded in the Endodontidae (Solem 1976) and some Australian Charopidae (Stanisic 1990). The closed tube or distinct groove assist water conservation by obviating the need to use pallial water to eliminate waste products. At the same time, water is presumably resorbed from the excretory products along the entire length of the secondary ureter.

The development of a closed secondary ureter has been considered a major advance in land snail evolution and a necessary pre-adaptation for the development of terrestrial slugs (Solem 1978a).

Respiration

A major characteristic of pulmonates is the development of a pulmonary cavity (pulmonary sac or 'lung') from the pallial cavity (Figs 14.19A, 17.2A). The anterior mantle edge has fused to the foot and neck and there is only a small opening to the exterior – the pneumostome. Although a shell may be absent, the mantle cavity invariably maintains an anterior position. The mantle skirt, which forms the roof and sides of the pulmonary cavity is highly vascular, and blood passes from it directly to the heart (Figs 14.19A, 17.11). The cavity thus functions as a lung in which the network of capillaries effects oxygen exchange and the muscles of the floor of the pulmonary cavity (dorsal body wall or diaphragm) allow its volume to be controlled. The small opening to the exterior (pneumostome) can be closed by a muscular sphincter.

In aquatic Basommatophora, respiration involves the lung, skin and secondary gills, but never true ctenidia (Haszprunar 1985). In the marine groups, Siphonariidae and Amphibolidae, the pulmonary cavity becomes filled with seawater and acts as a water lung. A secondary gill, consisting of epithelial folds, has developed within the mantle cavity of siphonariids (Fig. 14.19B). In freshwater groups respiration is essentially cutaneous and the respiratory function of the pulmonary cavity is reduced. The Planorbidae and Ancyliidae have developed a 'secondary gill' – through enlargement of the pallial fold. In the Ancyliidae which lack a pulmonary sac this gill is external; it is internal in the Siphonariidae and Planorbidae. An osphradium is present in limnic Basommatophora, but absent in terrestrial forms.

Among systellommatophorans, the intertidal Onchidiidae have a small pulmonary chamber which forms a vestibule for the anus (Fretter 1943). In contrast, the terrestrial Veronicellidae lack a mantle cavity and rely on cutaneous respiration.

Stylommatophorans typically have a pulmonary cavity with a well-developed vascular net and contractile pneumostome. The closed mantle cavity, in addition to its role in respiration, also acts as an important water storage area (Solem 1978a). Air is inhaled by opening the pneumostome and lowering the muscular floor of the cavity and although the pneumostome opens and

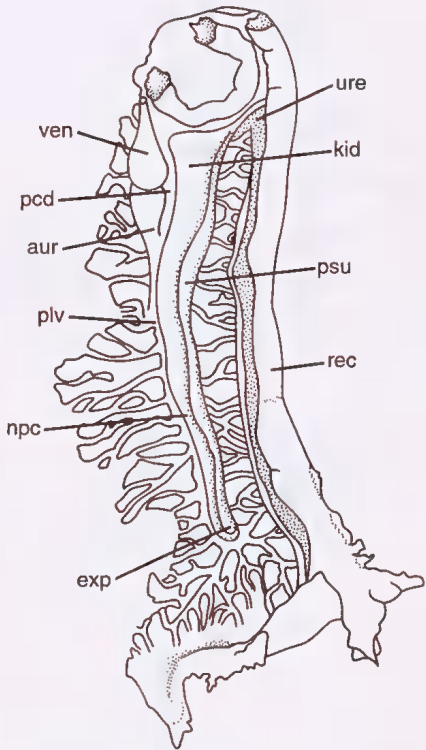


Figure 17.12 The pseudosigmurethrous ureter of *Amimopina macleayi* (Buliminidae). aur, auricle; exp, excretory pore; kid, kidney; npc, nephridial sac; pcd, pericardium; plv, pulmonary vein; psu, primary pseudo-ureter; rec, rectum; ure, ureter; ven, ventricle. (After Delhay & Bouillon 1972c) [C. Eadie]

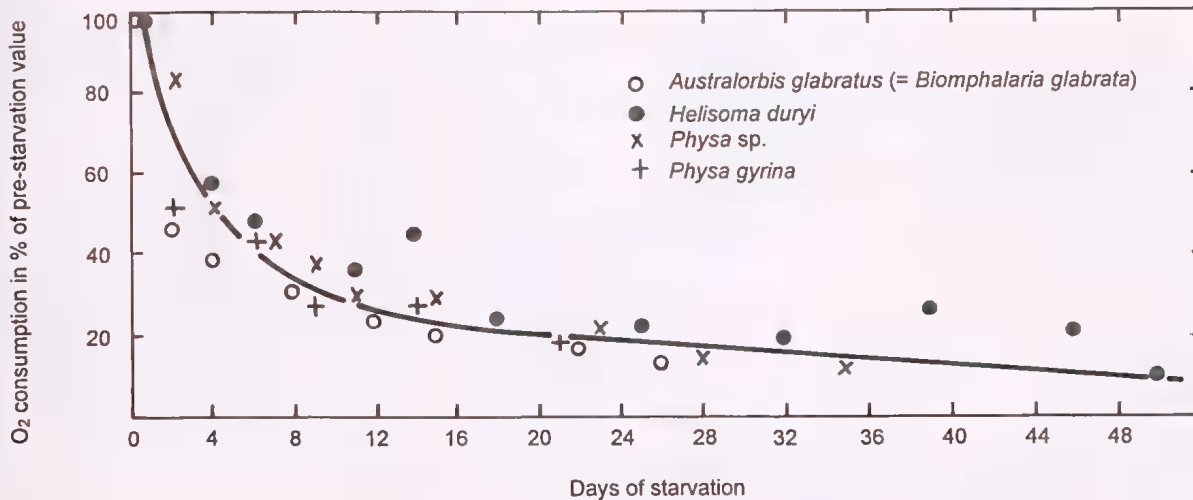


Figure 17.13 Effect of starvation on the rate of oxygen consumption of four pulmonate snail species. (Modified from Ghiretti & Ghiretti-Magaldi 1975) [C. Eadie]

closes in rhythmic sequence it is questionable as to whether each movement is related to respiratory ventilation (Ghiretti & Ghiretti-Magaldi 1975). Repetitive closing of the pneumostome may serve solely to reduce evaporation. Since the internal pressure of oxygen in the lung is lower than the ambient pressure, respiration by diffusion is also a possible mechanism for animals living at low metabolic levels.

Within the Stylommatophora, numerous variations on the typical mantle cavity form have arisen. In the Athoracophoridae, the pneumostome opens into a cavity from which numerous blind tubules extend into surrounding tissues in close association with blood vessels. The arrangement of the tubules is akin to the tracheal system of insects and although this arrangement is unusual, Solem (1959a, 1978a) considered that the 'tracheopulmonates' are merely highly modified sigmurethrans.

In more typical, derived slug-like taxa a discernible pattern of variation occurs (Solem 1978a; Tillier 1984a). Reduction in the visceral hump has caused compaction of the mantle cavity, resulting in relatively drastic changes in the arrangement of pallial organs. Compensation for the diminution of respiratory space takes two forms. Firstly, vascularisation of the remaining space is increased. Secondly, when compaction is severe, the available respiratory surfaces are increased in size either by internal rearrangement, as in the Athoracophoridae, or by the more commonly encountered condition seen in some semi-slugs (Tillier 1984a). In these, highly vascularised mantle lobes and shell laps, have evolved, thereby increasing the total gas exchange area (Solem 1978a).

Efficiency of respiration also depends on the oxygen-carrying capabilities of the respiratory pigments present. The only pigments that occur in pulmonates are haemocyanins and haemoglobins (Ghiretti & Ghiretti-Magaldi 1975). Among the pulmonates studied, most have haemocyanins. Several species lack respiratory pigments. Haemoglobin is present only in the Planorbidae, but its oxygen carrying capabilities are low and oxygen transport in these species is more likely to be dependent on the rapid movement of body fluids from the respiratory surface to the tissues and back (Ghiretti & Ghiretti-Magaldi 1975).

Among pulmonates, metabolic rates do not vary greatly from species to species, but oxygen consumption varies extensively (Table 17.2; Ghiretti & Ghiretti-Magaldi 1975). The rate of oxygen uptake during aestivation is not known, but is probably minimal. Other factors, such as physiological activity and biochemical changes in body tissues due to seasonal influences, can also affect oxygen uptake (Fig. 17.13).

Sense Organs and Nervous System

Pulmonates are euthyneurous. The central nervous system is detorted, and the ganglia are concentrated into a ring around the digestive tract. However, traces of chiasmoneury in which connectives are crossed, are present in some Basommatophora, for example, the Ellobiidae. The degree of chiasmoneury is variable. In higher pulmonates, such as the Helicidae, the various circumoesophageal ganglia are highly condensed and the connectives between them very short, but there is much variation among stylommatophoran pulmonates (Tillier 1989). In some basommatophorans, for example, the genera *Lymnaea* and *Chilina*, the various ganglia are well separated, but in others there is a tendency for shortening of connectives and fusion of ganglia (Fig. 17.14; Hubendick 1978).

Bargmann (1930) detailed the visceral nerve chain of pulmonates and concluded that eight types can be recognised. On the basis of functional cerebral-ganglion morphology, Van Mol (1967) proposed four main groupings – Archaeopulmonata (Ellobiidae, Otinidae), Basommatophora (remaining families), Soleolifera and Sigmurethura (all stylommatophoran families). Haszprunar & Huber (1990) recognised three basic types which define the Basommatophora, Systellommatophora (Gymnomorpha and Otinidae), and a new order, the Eupulmonata (= Trimusculidae, Ellobiidae, Stylommatophora). Tillier (1989) surveyed the visceral-chain morphology of most stylommatophoran families, and Emberton (1991) surveyed 17 stylommatophoran subfamilies, obtaining data which conflict in part with those of Tillier (1989).

In *Helix aspersa*, the circumoesophageal ring consists of nine ganglia and their connectives (Fig. 17.14C). The main ganglia are two cerebral ganglia, two pedal ganglia, two pleural ganglia, two parietal ganglia and an unpaired visceral ganglion (Hyman 1967). Additional ganglia connected to the oesophageal ring are the buccal ganglia and the tentacular ganglion. The ganglia forming the ventral part of the visceral ring are fused and consist of two pleural ganglia, two parietal ganglia, and a visceral ganglion (Fig. 17.14C); this pentaganglionate condition of the so-called visceral ring is also seen in opisthobranchs (Haszprunar 1985). Van Mol (1967, 1974) identified the procerebrum as the main synapomorphy of pulmonates. The procerebrum is assumed to be homologous with the rhinophoral gland of the Opisthobranchia (Haszprunar & Huber 1990) and has a neurosecretory function. It comprises small, globineurous cells, or large cells, or both (Van Mol 1967, 1974), features that correlate with modes of breathing. Contrary to the view of Van Mol (1967, 1974), Haszprunar & Huber (1990) considered the presence of large cells as primitive in the Pulmonata.

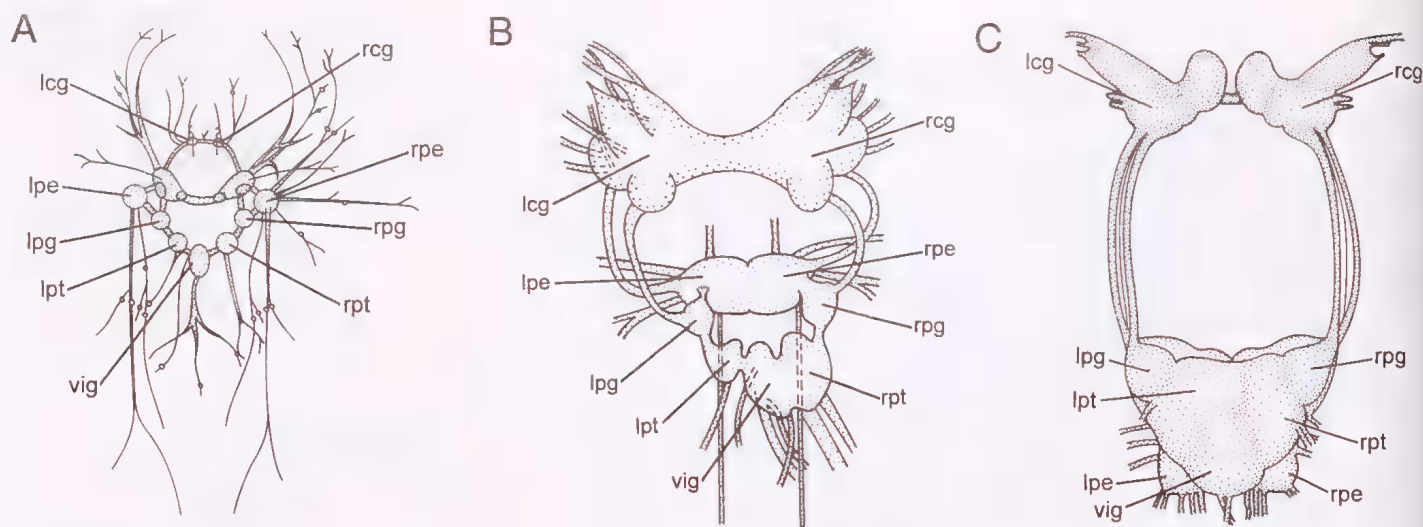


Figure 17.14 The circumoesophageal ganglia exhibit varying degrees of fusion. **A**, *Lymnaea* sp. (Lymnaeidae), in which the ganglia are all discrete. **B**, *Stenogyra* sp. (Subulinidae), exhibiting a moderate degree of fusion. **C**, *Helix* sp. (Helicidae), exhibiting the maximum extent of fusion. lcg, left cerebral ganglion; lpe, left pedal ganglion; lpg, left pleural ganglion; lpt, left parietal ganglion; rcg, right cerebral ganglion; rpe, right pedal ganglion; rpg, right pleural ganglion; rpt, right parietal ganglion; vig, visceral ganglion. (After Kerkut & Walker 1975)

[C. Eadie]

Two additional neurosecretory centres are closely associated with the cerebral ganglion in the Pulmonata – the cerebral gland and the dorsal bodies. The presence of the cerebral gland is a synapomorphy for the pulmonate group, but is internalised in various lines (Van Mol 1967, 1974). The dorsal bodies are constant in shape and structure throughout the Pulmonata but display variability in innervation among the various subgroups (Boer, Slot & Van Andel 1968; Vincent, Griffond, Wijdenes & Gomot 1984).

The nerve trunks emanating from a particular ganglion may indicate its functional role, but the pattern of nerves radiating from particular ganglia varies from species to species. In some taxa, the cell bodies for a particular nerve axon are not necessarily within that ganglion; they may be situated in another ganglion, some distance away, as a result of condensation (Kerkut & Walker 1975).

The ganglia are covered by the epineural sheath, composed of dense, tough, white connective tissue, and each ganglion is supplied by symmetrically arranged arteries from the anterior aorta. A number of compounds, including those which are considered to be transmitter agents, have potent actions on pulmonate neurones. Studies have indicated similarities between pulmonate neurone receptors and the neurone receptors of other animal groups and there is strong evidence that acetylcholine is a transmitting agent between neurones in the pulmonate central nervous system (Kerkut & Walker 1975).

The major pulmonate sensory organs are the tentacles, eyes (Fig. 17.15) and statocysts (Fig. 17.16). The tentacles are either invaginable or contractile (Fig. 17.4) and their mode of function has been used by some authors to imply possible affinities between groups (for example, Burch & Patterson 1969).

The retractor muscle which invaginates the optic tentacle of stylommatophorans is a branch of the columellar muscle. It is covered with a thick cuticle overlying a columnar epithelium penetrated by the numerous distal neurosensory cell processes (Hyman 1967).

The single pair of tentacles present in the Basommatophora (Hubendick 1978) are contractile and are typically slender, cylindrical and pointed. The tentacles are reduced in certain marine groups. Within the Ellobiidae a pair of papillae present on the dorsal surface of the snout has been interpreted as a second pair of rudimentary tentacles.

Pulmonate eyes are vesicular, converse, and located either at the base of the tentacles (Basommatophora) or at or near the tip of the superior tentacles (Stylommatophora). The cornea is formed by

flattened and transparent epidermis and the retina is composed of pigment and retinal cells (Fig. 17.15; Hyman 1967). The retinal cells are sensory and give rise to a nerve fibre which penetrates the connective tissue of the eye capsule before becoming part of the optic nerve. There is no optic ganglion (Kerkut & Walker 1975).

Pulmonate statocysts are generally situated laterally between the pleural and pedal ganglia. They are spherical in shape, covered by a layer of connective tissue and lined by hair-bearing epithelial cells; the lumen is filled with fluid and calcareous statoliths (Fig. 17.16; Kerkut & Walker 1975).

Reproduction

Pulmonates are hermaphrodites. The reproductive system is complex and variable (Figs 17.17, 17.18A), but conforms to a basic plan (Fig. 17.2C). The variability arises partly because the reproductive system is free to coil within the haemocoel (Duncan 1975). This allows for changes in the shape and size of various structures and the addition of various flagella, caeca and sacs to the basic reproductive system without the need for major spatial adjustments.

In some basommatophorans, the ovotestis is located in the visceral hump with the digestive gland. Protandric hermaphroditism is common among the more primitive forms (Hubendick 1978), whereas advanced groups, including the Lymnaeidae, display simultaneous hermaphroditism (Geraerts & Joosse 1984).

A hermaphroditic duct, which may have one or more seminal vesicles attached, conducts the gametes to the fertilisation pocket at the base of the albumen gland. This region – the fertilisation pouch–seminal receptacle complex – including the carrefour region, is variable in structure. The subapical genitalia display variability in the extent of separation of the male and female ducts. In some species, such as *Pythia scarabaeus* and *Ovatella myosotis*, the genital duct is incompletely divided into 'semi-canals' (see Hubendick 1978). The female and male tracts are lined with glandular epithelium and prostatic epithelium, respectively. Gonopores are separate and the vas deferens is connected to the genital vestibule by an open ciliated groove. The spermatheca is inserted on the vagina.

In the Amphibolidae and Siphonariidae the hermaphroditic duct is long with a single lumen and there is a single genital pore in the typical anterior male position.

The freshwater basommatophorans have separate male and female ducts and the prostate gland is a series of invaginations of the male duct. The male copulatory organ (Fig. 17.18B, C) comprises a sheathed penis traversed by the vas deferens, frequently with a

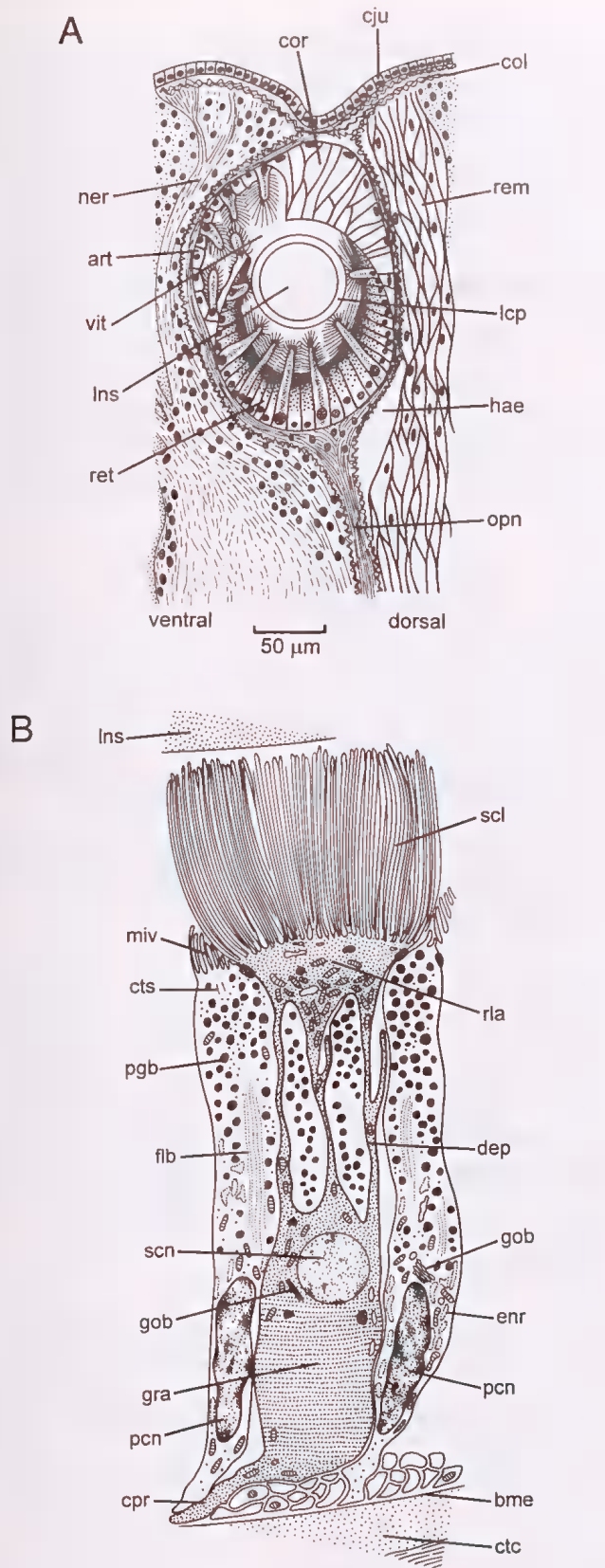


Figure 17.15 A, the eye of *Agriolimax* sp. (Limacidae), in longitudinal section, showing the main features. B, the fine structure of the retina of *Helix pomatia* (Helicidae), a sensory cell is shown surrounded by a pigment cell; the peripheral processes of the sensory cell join to form a receptor lamella from which projects the striated border; the central process arises from the base of the sensory cell. art, 'accessory retina'; bme, basement membrane; cju, conjunctiva; col, collagen; cor, cornea; cpr, central process; ctc, connective tissue capsule; cts, centrosome; dep, 'dendritic process'; enr, endoplasmic reticulum; fib, filament bundle; gob, golgi body; gra, granules or vesicles in base of sensory cell; hae, haemocoel; lcp, lens capsule; lns, lens; miv, microvilli; ner, tentacular nerve; opn, optic nerve; pcn, pigment cell nucleus; pgb, pigment body; rem, retractor muscle; ret, retina; rla, receptor lamella; scl, sensory cells; scn, sensory cell nucleus; vit, vitreous body. (After Kerkut & Walker 1975) [C. Eadie]

distal extension called the praeputium. A number of major penis types, each with its own set of variations, have been recorded (Hubendick 1978).

The Systellommatophora have the male and female genital openings separate. The male opening is situated at the anterior end of the animal and the female gonopore is located posteriorly either in the pedal grooves or the hyponotum. In the Onchidiidae the female opening is adjacent to the anus at the posterior end of the animal. Additional structures include dart glands in some onchidiids and a penial (Simroth) gland in the Rathouisiidae. The penis of veronicellids has a 'stimulator' (Bishop 1977).

The stylommatophoran ovotestis consists of a single or multiple group of follicles situated in the apical whorls of the digestive gland. Simultaneous hermaphroditism is typical though protandry has been recorded in several groups including some Australian camaenids (Solem & Christensen 1984). However, in terms of the differentiation of the primary gametes they are probably also simultaneous hermaphrodites. A coiled hermaphroditic duct connects the gonads to the carrefour region which varies in detail from family to family (Bayne 1973; Tompa 1984).

The structural arrangement is simple and similar in the Endodontidae and Charopidae (Solem 1976; Staniscic 1990). The carrefour region is a barely noticeable swelling in the gonoduct, partially buried in the albumen gland, and receives ducts from the gonad (hermaphroditic duct), talon and albumen gland. A separate duct exits to the prostate-uterus complex. The gonoducts distal of the carrefour region may be separate or fused. Solem (1972a, 1976) considered that having fused pallial gonoducts is a derived condition, and is a recurrent trend within the Stylommatophora. Duncan (1960) held an opposite view, stating that a single fused duct was followed by separation and specialisation of the male and female tracts. Tompa (1984) suggested that evolution of fused and separate tracts may be related to egg retention and the development of ovoviviparity in various pulmonate groups. In the Partulidae, other orthurethrans and the Succineidae there is partial fusion of the tracts. In the Charopidae, and most zonitids and helicoidean taxa, there is almost complete fusion of the gonoducts. In those groups with separate gonoducts the prostate gland is a thin tube and receives ducts from a number of prostatic alveoli which are usually arranged along its length in a specific pattern. Where the prostate gland and uterus are fused, as in the Charopidae, the prostatic duct, into which the prostatic alveoli discharge, is a lateral outpocket of the common gonoduct lumen. The uterus is a sac-like structure which may be differentiated along its length (Solem 1976; Staniscic 1990).

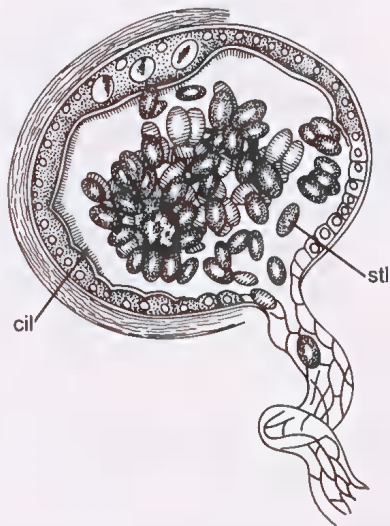


Figure 17.16 Structure of the pulmonate snail statocyst. cil, cilia; stl, statoliths. (After Kerkut & Walker 1975) [C. Eadie]

17. PULMONATA

The terminal female genitalia consist of a relatively short muscular tube (= free oviduct) that gives rise to a muscular vagina. The stalk or duct of the spermatheca which enters the vagina or atrium, varies from long (as in charopids) to very short (as in enids). In the male genitalia the vas deferens leaves the prostate gland and either enters the penis directly, or expands to form a non-eversible muscular epiphallus which enters the penis through a simple pore or elaborate verge. The epiphallus assists in spermatophore formation.

The penis (Fig. 17.18B) is usually a muscular tube, often with a muscular sheath, and internal pilasters which show extensive structural variation particularly among sympatric congeneric species (Solem 1976, 1992; Emberton 1988, 1991; Stanicic 1990). A penial retractor muscle inserts on the penis or epiphallus. The penis may be reduced or absent (aphally) in some orthurethran and non-orthurethran groups (Cooke & Kondo 1960; Pokryszko 1987; Baur & Chen 1993). In these species the genital apertures are opposed at copulation.

In addition to the basic set of reproductive structures there are accessory mucous glands, dart sacs, appendices and flagella which have been derived independently in various taxa (Solem 1978a; Tompa 1984).

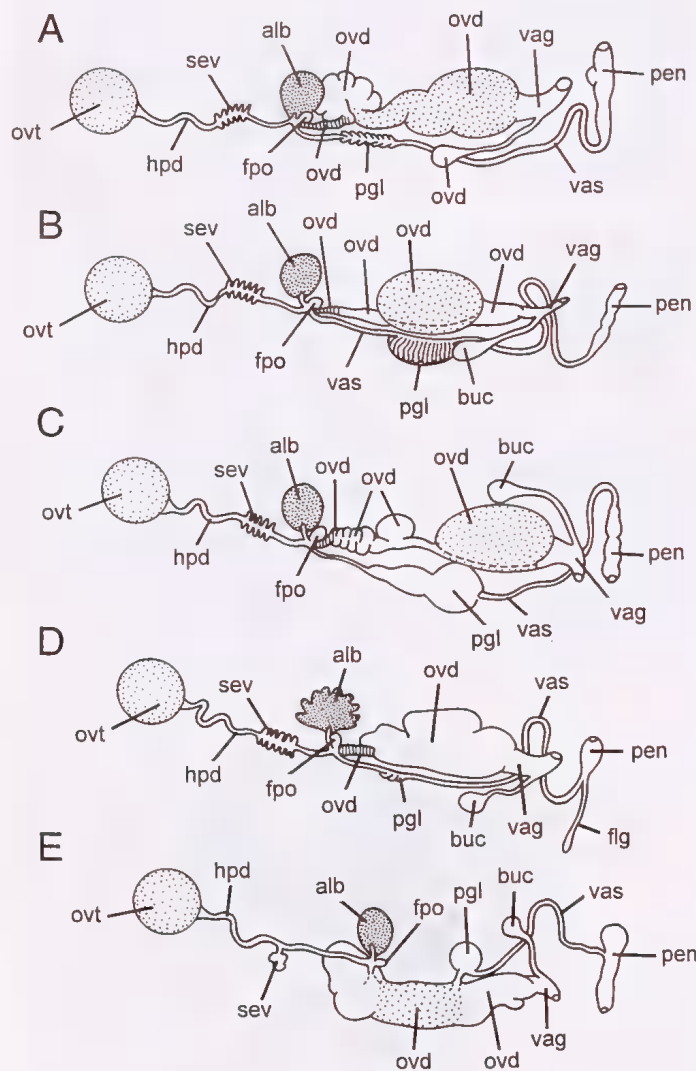


Figure 17.17 The organisation of the reproductive systems of representatives of freshwater basommatophoran families. Homologous organs of the female tract are shown by different shading. A, *Physa fontinalis* (Physidae). B, *Planorbarius corneus* (Planorbidae). C, *Lymnaea peregra* (Lymnaeidae). D, *Ancylos fluvialis* (Ancyliidae). E, *Acroloxus lacustris* (Acroloxidae). alb, albumen gland; buc, bursa copulatrix; flag, flagellum; fpo, fertilisation pocket; hpd, hermaphroditic duct; ovd, oviduct; ovt, ovotestis; pen, penis complex; pgl, prostate gland; sev, seminal vesicle; vag, vagina; vas, vas deferens. (After Duncan 1975) [C. Eadie]

In advanced taxa such as helicoideans the use of 'love darts' in the mating ritual has most probably developed to ensure successful coupling, and among the limacoideans, complex courtship procedures presumably have a similar purpose. Special recognition features include the stimulatory structures on the functioning surface of the penis and vagina, and head warts which are present in some advanced helicoids, African urocyclus and some camaenids (Tompa 1984; Solem 1985a, 1992).

Transfer of sperm may involve an exchange of unorganised sperm masses, or the transfer of distinctive chitinised envelopes of sperm or spermatophores (Solem 1974, 1978a). These sperm packets have variable and often complex species-specific shapes (Solem 1974).

Mating can take some time, and snails may be united for several hours (Tompa 1984). Fertilisation is usually reciprocal, although self-fertilisation has been reported in some species (Whitney 1940). In populations with aphyallic individuals it is possible that self-fertilisation may be favoured over cross-fertilisation (Tompa 1984).

Compared with the eggs of most other gastropods, those of stylommatophorans are few in number, extremely yolky and sometimes quite large. The egg shell is elastic and partly or completely calcified, but not impermeable to water and the hazard of desiccation is partially obviated by behavioural adaptations which ensure oviposition in damp, shaded places or in the soil. Retention of the egg and subsequent birth of live young are also efficient adaptations for avoiding desiccation. Oviparity (egg laying) is most common but ovoviviparity and viviparity have been recorded for numerous species (Tompa 1979).

Most basommatophoran young hatch as crawling snails (Geraerts & Joosse 1984), but free swimming larvae are produced in some families such as the Amphibolidae, Onchidiidae (Raven 1975) and the Ellobiidae (Morton 1979).

Pulmonate ova are generally small and poor in yolk. When they are laid, each is surrounded by an egg capsule filled with albumen. In freshwater groups, these capsules are usually combined into a common mass by an outer membrane or jelly. In contrast, land pulmonates lay single eggs that are usually surrounded by a calcareous membrane (Fig. 1.20H; Raven 1975).

Egg formation is follicular and growth proceeds in two stages. Previtellogenesis leads to an increase in the amount of protoplasm and is followed by an accumulation of yolk (vitellogenesis). The yolk and egg capsule fluid (albumen) contain proteins and polysaccharides which play an important role in embryonic nutrition (Raven 1975).

Maturation of the pulmonate egg leads to the formation of the female pronucleus and involves two maturation spindles. The formation of the first maturation spindle is relatively similar in most taxa that have been studied, but four different ways in which the secondary maturation spindle is formed can be distinguished (Raven 1975).

Spermatogenesis and spermatozoa have been examined at the fine structural level in a number of pulmonate groups (Systellommatophora, Basommatophora and Stylommatophora: for reviews and principal references see Thompson 1973; Healy 1983, 1986; Healy & Jamieson 1989; Griffond Dadkhah-Teherani, Medina & Bride 1991). The spermatozoa (Fig. 17.19) most closely resemble those of opisthobranchs and certain 'alogastropod' groups such as the Pyramidelloidea, Rissoelloidea and Omalogyroidea (Healy 1993, 1996). Characteristic features of this type of internally fertilising spermatozoon include a distinctive acrosomal complex (consisting of a round vesicle supported basally by a columnar pedestal), a helical nucleus and a helical, highly elongate midpiece. In the midpiece, the 9 + 2 pattern axoneme is associated with nine coarse fibres (showing striated substructure) and enveloped by a complex mitochondrial derivative composed of matrix and paracrystalline layers and one or more enclosed, glycogen-filled helical spaces – the glycogen helices. A glycogen piece usually occurs posterior to

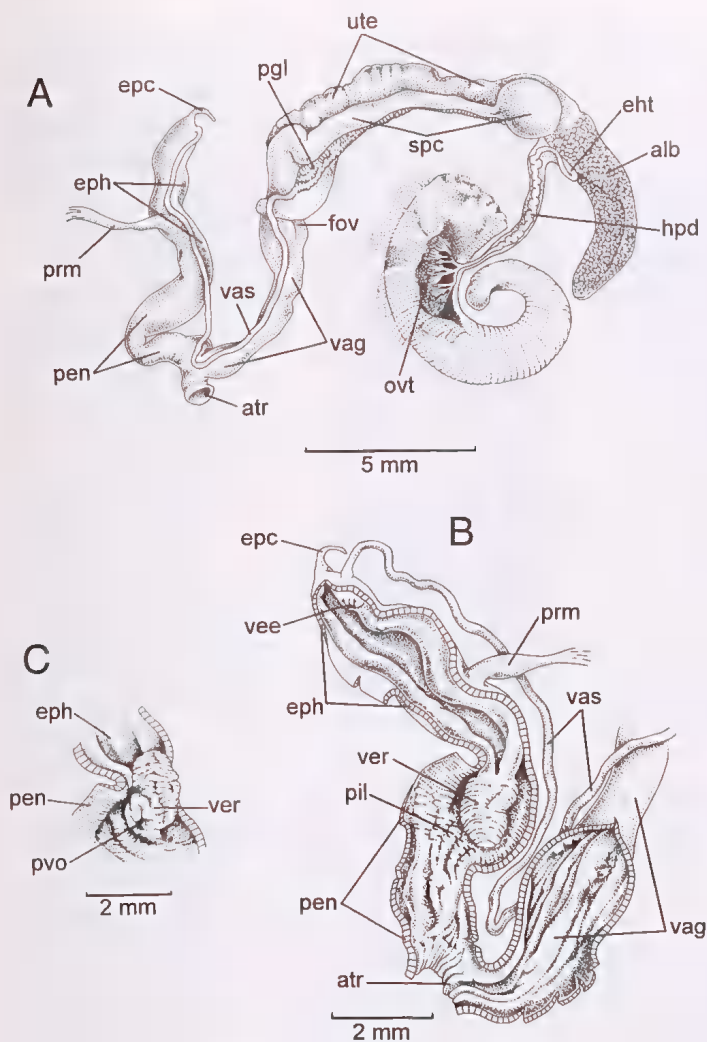


Figure 17.18 Genitalia of *Semotrachia esau* (Camaenidae). **A**, whole reproductive system; **B**, the interior of the epiphallus, penis and vagina; **C**, detail of verge. **alb**, albumen gland; **atr**, atrium; **eht**, entrance of hermaphroditic duct into talon; **epc**, epiphallus; **eph**, epiphallus; **fgv**, free oviduct; **hpd**, hermaphroditic duct; **ovt**, ovotestis; **pen**, penis; **pgl**, prostate gland; **pil**, pilaster; **prm**, penial retractor muscle; **pvo**, opening of verge into penis; **spc**, spermatheca; **ute**, uterus; **vag**, vagina; **vas**, vas deferens; **vee**, vas deferens entering epiphallus; **ver**, verge. (After Solem 1993) [R. Plant]

the midpiece, but is evidently absent in stylommatophoran pulmonates (Healy & Jamieson 1989; Giusti, Manganelli & Selmi 1991). Pulmonate taxa at and above the generic level show substantial differences in morphology of the acrosomal complex, nuclear keels and midpiece glycogen helices – to such an extent that sperm features have proved of taxonomic and potential phylogenetic usefulness (Thompson 1973; Healy 1983, 1988a, 1988b, 1996).

Embryology

Fertilisation in pulmonates involves the penetration of a single or of several sperm (polyspermy) into the egg. If more than one sperm enters, only one forms a pronucleus and the others eventually break down. The male pronucleus does not form until the second polar body is extruded. When male and female pronuclei come into close proximity, a spindle forms between them, the nuclear membranes of the pronuclei dissolve and their chromosomes become arranged in the first cleavage spindle (Raven 1975).

The egg undergoes determinate spiral cleavage (Raven 1975) and the coeloblastula develops following the formation of a small lumen in the blastula. Gastrulation is embolic and the archenteron

is formed from the four primary endoderm cells. The blastopore becomes the mouth or site of stomodeal invagination and much of the stomodeum forms the oesophagus. The radular sac is a ventral invagination of the oesophagus. The foot arises as a protuberance below the mouth and a circular area of ectoderm gives rise to the shell gland which secretes a cap-like shell of organic material (Hyman 1967; Verdonk & Biggelaar 1983).

The pulmonate embryo has several structures which regress before hatching. These include the cephalocyst which accommodates the albumen sac, the podocyst which may be circulatory in function, and the protonephridia which have different origins in basommatophorans and stylommatophorans.

The mantle is formed from the shell gland. The shell is cup-shaped at first but becomes spirally coiled through more rapid growth on one side. In shelled pulmonates, the shell continues to grow and the mantle cavity originates as an invagination under the mantle which becomes closed by fusion to the neck region. In slugs, such as *Arion* and *Limax* species, the shell is encapsulated by the mantle and remains in a rudimentary condition. In *Onchidella celtica* the larval shell and larval operculum are shed at metamorphosis (Fretter 1943).

The stomach and crop develop from the archenteron and the pericardium, heart, and definitive nephridium develop from the mesodermal bands of the archenteron. In *Achatina fulica* these organs develop from the right mesodermal band (Ghose 1963), whereas the left band is involved in the basommatophoran *Planorbarius corneus* (Pötzsch 1904). Blood sinuses arise as spaces in the mesenchyme.

The nervous system is derived from the ectoderm and the ganglia are formed by proliferation of ectodermal cells that sink to the interior. The commissures and connectives are formed by secondary outgrowth from the ganglia.

The great majority of pulmonates hatch as young snails which are anatomically complete except for their reproductive system which originates as a single ectodermal invagination of the mantle cavity in the Stylommatophora. In the Basommatophora two separate primordia are involved (Fraser 1946). The reproductive structures are a system of vague tubules at birth and develop to maturity quite rapidly in some freshwater groups, but can take one to several years in some terrestrial species.

NATURAL HISTORY

Life History

Very little is known about the life histories of Australian pulmonates and available information is largely anecdotal. Most studies have been taxonomic, especially so for marine and freshwater species.

McLauchlan (1951) detailed the life cycles of several land snails from the Sydney region, New South Wales, and included incidental notes on the growth and habits of some Queensland species. Egg laying was documented for species of *Vercularion*, *Strangesta* and *Meridolum*, although some *Meridolum* species were reported to produce live young.

Kimberley camaenids, living in a highly seasonal monsoon climate with unpredictable wet seasons, have a four year maturation period before life as a true hermaphrodite (Solem & Christensen 1984). *Amplirhagada* species reach half adult size in the wet season of birth, attain adult size and become mature males at the end of their second wet season and function as males at the beginning of the third wet season. The female genitalia do not mature until the end of the third wet season. Hence the snail does not function as a hermaphrodite until the fourth and subsequent years. This specialised life cycle was probably derived from a more general pattern present among monsoonal land snails (Solem & Christensen 1984).

17. PULMONATA

Adaptations to the monsoonal climate include morphological changes which may be peculiar to this fauna. The size of the ovotestis and hermaphroditic duct reduce midway through the wet season, probably to allow for increased nutrient storage before dry-season aestivation. Allosperm, produced during the wet season, are not immediately digested but are stored until late in the following dry season. This may contribute to more efficient sperm production in the following season or provide an additional source of nutrients for the snail. In addition, the species have the ability to respond rapidly to the onset of rain, leading to a frenzied pattern of feeding, mating and egg laying (Solem & Christensen 1984).

Growth in a monsoonal climate can be sporadic due to the variability of rainfall. Although the Kimberley camaenids reach adulthood at the end of their second wet season, the length of feeding activity, which is governed by the rains, varies from year to year and affects the final adult size in populations. In shorter and drier wet seasons and in situations where snails live in poor moisture-retaining microhabitats, the adult size of individuals is smaller because the snails become adult at a lower whorl count. In contrast, favourable moisture conditions allow extended growth time and greater numbers of whorls, and hence, larger individuals.

The seasonal adaptations and changes that have been documented for Kimberley land snails, could have application to many other Australian snail species. The seasonally related size differences reported by Solem & Christensen (1984) have been noted in Queensland land snails that inhabit the northern monsoon forests and those living in the seasonally dry subcoastal vine thickets of mid-eastern and south-eastern Queensland (J. Stanisic personal observation).

Data on longevity of Australian pulmonates are virtually non-existent. A life span of greater than eight years was postulated for Kimberley camaenids (Solem & Christensen 1984). Solem (1982) predicted a two year life cycle for the Kimberley helicarionid *Westracystis lissus*, based on presence of different size morphs among some populations of this species. McLauchlan (1951) estimated a life expectancy of six to seven years for some *Strangesta* species and McMichael & Iredale (1959) reported that specimens of the northern Queensland camaenid, *Chloritisanax banneri*, came to life after six years in a box at the Australian Museum.

Ecology

Australian Pulmonata can be divided into three basic ecological groups – marine, freshwater and terrestrial. With few exceptions basommatophorans are aquatic. The Ellobiidae (with a few terrestrial exceptions) and Amphibolidae are largely confined to mangroves (Fig. 1.47) or saltmarshes with some species on high energy shores in the supralittoral or upper littoral zones, whereas the limpet-like Siphonariidae and Trimusculidae are rocky shore dwellers. The higher limnic Basommatophora, which include the Lymnaeidae and Planorbidae, are found in both lentic and lotic freshwater environments and some, such as the Lymnaeidae, prefer mainly lentic habitats (slow or non-flowing waters) and even thrive under eutrophic conditions (Smith & Kershaw 1979). Freshwater species attach to weed and other suitable substrata such as rocks and timber and generally feed on algae. *Smeagol* species live among gravel and pebbles in the upper littoral zone (Tillier & Ponder 1992).

The Systellomatophora includes the marine Onchidiidae and two terrestrial slug families. Stylommatophorans are exclusively land dwellers.

Retention of moisture is the primary physiological problem for land snails. Hence in eastern Australia the majority of the land pulmonates are found in closed forests (= rainforest) where moisture levels in the form of rainfall and humidity are high. These forests also provide ample food and shelter. Comparatively few east coast species have made the transition to the drier eucalypt forests. In the arid parts of central and Western Australia snails live in isolated, moisture-conserving microhabitats and rely on patchy, predictable but variable monsoonal rains for survival.

In each situation, the faunas are peculiarly adapted to their environment. Reproductive and behavioural strategies allow several species to survive in a single pile of rock talus in the Kimberley (Solem & Christensen 1984; Solem 1985b). In the eastern rainforests, snail diversity is high and slugs and semi-slugs have evolved. These species have reduced their dependence on the moisture-conserving features of a shell in response to relatively continuous high rainfall.

Limestone outcrops are also important refugia for land snails, particularly in eastern Australia and the Kimberley. In eastern Australia the outcrops frequently occur among drier sclerophyll forests, but the rocks trap available moisture in crevices and provide protection from wildfires. In these habitats, peculiar snail communities, often remarkably different from those in the surrounding forests, have developed. The land snails (Fig. 17.20A) that inhabit these exceptional refugia benefit from an ample supply of calcium and, because of long term isolation and the need to adapt to life among and on rocks, show shell and radular specialisations (Stanisic 1990).

Popularly, Australian land snails have been segregated into tree and litter species. Although the former is a practical category, the latter encompasses groups with a number of significantly different microhabitat preferences. For example, the 'litter-dwelling' Charopidae live on trees, rock surfaces, among moss, under bark, under logs and among dirt particles (Stanisic 1990). These microhabitat preferences are often significant systematically at both the generic and species levels.

Snails exploit a wide range of microhabitats in rainforests. Arboreal species include members of the Achatinellidae, Enidae, Helicarionidae, Charopidae (*Hedleyoconcha*, *Oreokera*), Cystopeltidae, and Camaenidae (*Bentosites*, *Chloritisanax*, papuinines; Fig 17.20B). They may live on trunks and branches of trees (Enidae, papuinines), under bark (*Chloritisanax*) or on leaves (*Hedleyoconcha*, Achatinellidae). *Triboniophorus graeffei* (Athoracophoridae) and Cystopeltidae live on the ground but forage on rocks and tree trunks at night.

The microhabitats of most ground-dwelling rainforest species have not been well documented and much of the available information is anecdotal and based on inference from few examples. Charopids have diverse microhabitat preferences (listed above). Helicarionids live under logs (*Melocystis*, *Helicarion sensu lato*; Fig. 17.20D), arboreally or among leaves in litter (*Nitor*). Some helicarionids are ground-dwelling but forage on the leaves and trunks of shrubs and trees. Rhytidids appear to live free in the litter/soil layer under logs. *Pedinogyra* (Caryodidae) and *Coelocion* (Megaspiridae) species live in litter among rock talus. Camaenids demonstrate an equivalent microhabitat diversity to that of charopids. Species of *Austrochloritis sensu lato*, *Meridolum* and *Galadistes* species seem to prefer living under logs. *Torresitrachia* and *Hadra* species (Fig. 17.20C) live either under rocks or logs, and species of *Trachiopsis* live in the top layer of litter and soil under logs and rocks. The minute pupilloid snails usually seal to the underside of logs, rocks, or bark on trees (*Pupisoma* species).

In central and western Australia, camaenids are usually associated with rock talus or vegetation clumps such as spinifex, and live buried deep in the talus or in soil, emerging only in response to the onset of rain.

Limestone outcrops provide a secondary, above-ground habitat and species such as the pupillid *Gyliotrachela australis* and some charopids (Stanisic 1990) live attached to the limestone rock, usually along driplines and in shaded areas.

The feeding habits and dietary preferences of the terrestrial pulmonates are poorly understood. The literature abounds with references to detritivores and fungivores. These terms have been loosely applied to entire groups of snails (Colman & Burch 1977) but not usually on the basis of direct observations of individual species.

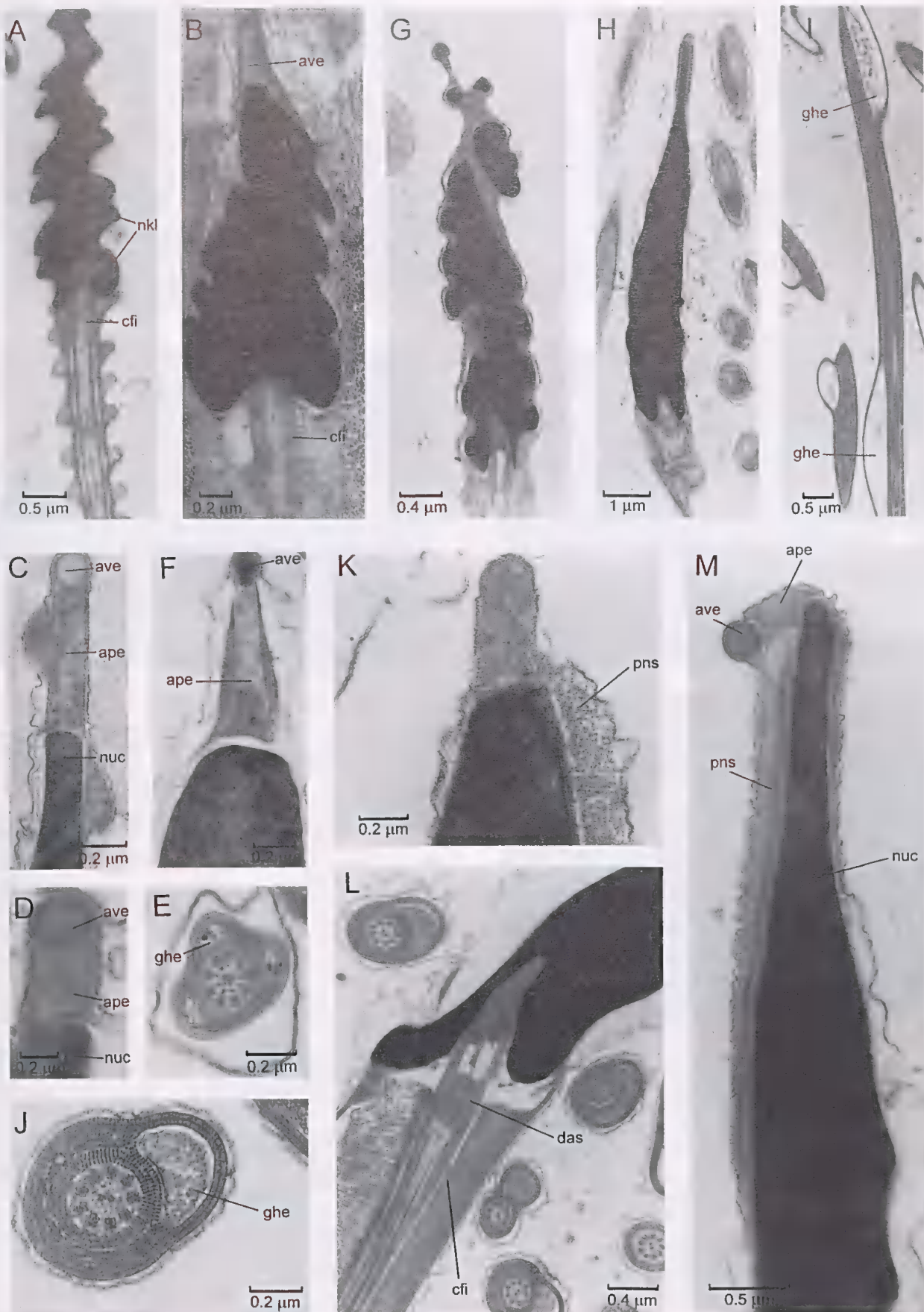


Figure 17.19 Pulmonate sperm ultrastructure. **A**, *Ophicardelus ornatus* (Ellobiidae), nucleus and portion of midpiece; **B**, *Austropeplea lessoni* (Lymnaeidae), acrosome, nucleus and portion of midpiece; **C**, *Salinator solida* (Amphibolidae), acrosome and nuclear apex; **D**, **E**, *Ophicardelus ornatus* (Ellobiidae), acrosome and transverse section of midpiece; **F**, *Onchidium damelii* (Onchidiidae), acrosome; **G**, *Helicarion australis* (Helicarionidae), nucleus; **H**, *Helix aspersa* (Helicidae), nucleus and portion of acrosome; **I**, *Helix aspersa*, spiralling glycogen helix in midpiece; **J**, *Sphaerospira bloomfieldi* (Camaenidae), acrosome and nuclear apex; **K**, *Sphaerospira yulei*, transverse section of midpiece; **L**, *Sphaerospira yulei*, longitudinal section of midpiece; **M**, *Helix aspersa*, acrosome and nuclear apex. **A**, **D**, **E**, Eupulmonata, Actophila; **B**, **C**, Basommatophora; **F**, Systellommatophora; **G**–**M**, Eupulmonata, Stylommatophora. **ape**, acrosomal pedestal; **ave**, acrosomal vesicle; **cfi**, coarse fibres; **das**, distal accessory sheath; **ghe**, glycogen helix; **nkl**, neck keel; **nuc**, nucleus; **pns**, perinuclear sheath. (**A**–**E**, from Healy 1983; **H**, **L**, **M**, from Healy & Jamieson 1989)

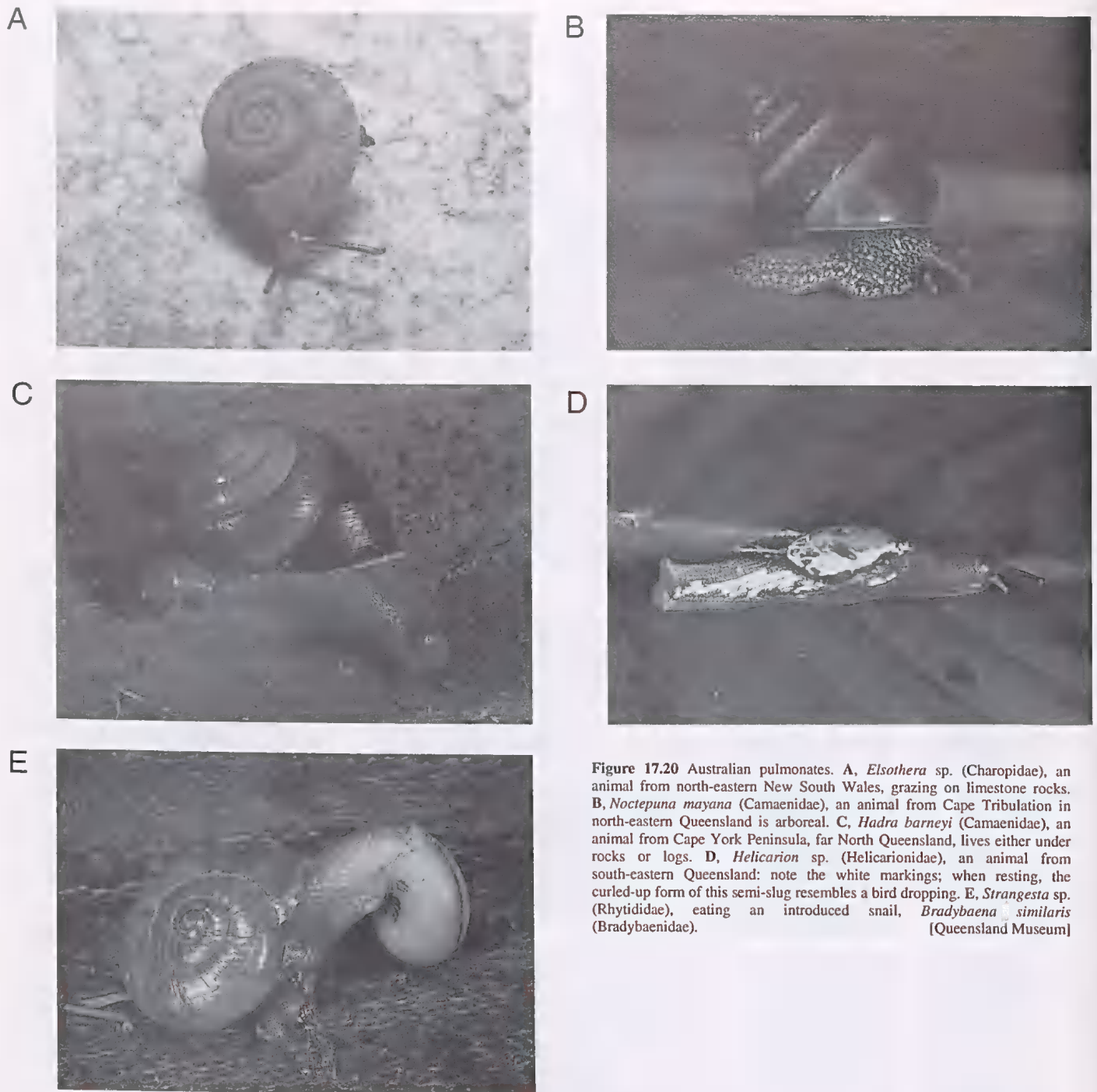


Figure 17.20 Australian pulmonates. A, *Elsothera* sp. (Charopidae), an animal from north-eastern New South Wales, grazing on limestone rocks. B, *Noctepuna mayana* (Camaenidae), an animal from Cape Tribulation in north-eastern Queensland is arboreal. C, *Hadra barneyi* (Camaenidae), an animal from Cape York Peninsula, far North Queensland, lives either under rocks or logs. D, *Helicarion* sp. (Helicarionidae), an animal from south-eastern Queensland: note the white markings; when resting, the curled-up form of this semi-slug resembles a bird dropping. E, *Strangesta* sp. (Rhytididae), eating an introduced snail, *Bradybaena* *similaris* (Bradybaenidae). [Queensland Museum]

McLauchlan (1951) reported that members of the carnivorous *Strangesta* feed on snails (Fig. 17.20E), worms and various other invertebrates. In the same study, a camaenid, *Meridolum* sp., was portrayed as an omnivore with a diet including vegetable matter, plant tissue, decaying vegetation and animal matter. Some charopids feed on microflora on limestone rocks (Stanisic 1990). Colman & Burch (1977) suggested that most are fungal feeders.

Feeding preferences, even within families, can be varied. In north-western Australia, species in the camaenid genera *Westraltrachia* and *Amplirhagada* are sympatric in limestone ranges. *Amplirhagada* species are generalised feeders on dead plant material. *Westraltrachia* species also feed on general plant debris except in limestone areas where they are sympatric with *Amplirhagada* species and graze on algal-fungal blooms on limestone seepage faces (Solem 1985b).

Cystopelta and *Triboniophorus* species and those helicarionids with arboreal habits probably feed on micro-algae and fungi that coat the stems, branches and leaves of trees. The Caryodidae are probably generalised feeders, although often caryodids have been collected while feeding on fungal mats under logs (J. Stanisic

personal observation). On the basis of their dagger-like radular tooth shape, the rathouisiid slugs are possibly carnivorous (Burch 1976a).

Predators of snails are varied but there are few literature references to actual observations of snail predation. Birds are certainly significant predators, particularly in the rainforests of southern Queensland. The Noisy Pitta (*Pitta versicolor*) utilises a stone (anvil) to break the shell of larger snails (Camaenidae, Caryodidae) before extracting the animal (J. Stanisic personal observation). Mammals (rats and carnivorous marsupials) and reptiles also probably eat snails. Ants are considered to be important predators in shaping of the Pacific Island snail faunas (Solem 1976) and probably are also major snail predators in most areas of Australia. Other invertebrate predators include carabid beetles (Bishop 1981), glow worms (Scott 1990) and carnivorous snails.

Habitat destruction associated with human activity is ecologically catastrophic for snails and forest clearing, limestone mining and the predilection to burn on a cyclic basis (Colman 1987) all can have major impacts on the ultimate survival of individual snails and even entire species.

Behaviour

Paramount to the survival of a terrestrial snail is the need to conserve water (Machin 1975; Solem 1978a). Even though this need is reduced in aquatic species, certain behavioural traits and morphological adaptations assist them in maintaining correct water balance. Some of the marine pulmonates, in particular those inhabiting intertidal habitats, have developed limpet-like shells which are clamped to the substratum during periods of exposure. They become active and feed only on damp rocks or when submerged. Estuarine forms, such as *Salinator* species and the Ellobiidae, burrow to avoid the effects of freshwater immersion. *Salinator* also has an operculum.

Some freshwater species burrow and aestivate (Hyman 1967) to avoid desiccation whereas others secrete an epiphragm.

Terrestrial species are much more susceptible to the effects of water loss and employ a variety of means to reduce the effects of desiccation. Most pulmonates do not have an operculum and although the majority of species are able to withdraw into the shell, they still suffer water loss through the soft mantle tissue which is exposed to the elements, as well as through the shell itself (Machin 1975). Some species aestivate by sealing to the substratum (logs, rocks, leaves, other snails). However, a proportion are free sealers and secrete a calcium-impregnated mucous shield – the epiphragm (Fig. 1.62) – across the aperture. This structure performs the same function as an operculum and reduces moisture loss although it is permeable to oxygen. Depending on the severity of local conditions, snails may secrete numerous epiphragms as they retreat further into the shell (Solem 1974). Some species living in drier areas burrow into the soil (for example, *Xanthomelon pachystylum*), whereas others move deeper into rock crevices or talus piles (Solem 1992).

Slug and semi-slug species do not have a shell in which to withdraw and have evolved such that their activity periods coincide with the humid periods of the day (early morning/early evening) or periods of rainfall (*Cystopelta* and *Helicarion* species). Not unexpectedly some of these slug species secrete extremely thick mucus which possibly has anti-desiccation properties. Helicarionid semi-slugs can also reduce water loss by curling up into a tight ball when resting, thus exposing much less of the body surface to the effects of evaporation.

Desert snails, in particular, need to have behavioural and physiological characteristics to survive the very high temperatures of their surroundings. Warburg (1965) showed that the mainly arid zone *Themapupa adelaidae* was able to survive for eight hours at 50°C.

Defence against predators is varied. Burch (1976a) suggested that some slugs secrete a noxious mucus which, when combined with visual cues provided by bright colouration, may offer protection from predators. Some helicarionids wriggle their tail vigorously when handled, possibly to draw attention from the more vulnerable visceral mass (Scott 1990). Some slugs break off their tail deliberately (autotomy) when disturbed, enabling the slug to crawl to safety while the predator attacks the wriggling tail piece: the tail region subsequently regenerates (Hyman 1967). This has not yet been reported in Australian species.

Although slugs do not have the protective advantage of the shell, they are less restricted in their choice of hiding places. Without the encumbrance of a shell they can slip into the narrowest of crevices to hide from predators.

Snails depend on a sense of touch coupled with behaviour patterns and possibly pheromones to find a suitable mate. This problem is compounded when closely related species live in the same area (Solem 1974), and accessory structures have developed to assist successful mating. In the introduced *Helix aspersa* mating involves the exchange of love darts whereas courting behaviour in some limacids is highly ritualised and complex (Tompa 1984). Some members of the Camaenidae, for example, *Rhagada*, have developed elaborate head warts (Solem 1985a) which are situated

between the superior tentacles. During mating these structures are intimately involved in the touching behaviour which is the lead-up to copulation. Head warts differ from species to species and presumably are species recognition devices.

Terrestrial pulmonates either produce live young or lay eggs that are subject to the same pressures of desiccation and predation as the adult snail. Few observations have been made on egg-laying behaviour. However, most land pulmonates are considered to lay clusters of rubbery eggs in depressions in the soil under logs or in rotting timbers (Tompa 1984). In contrast, *Strangesta* species and other rhytidids lay solitary, hard-shelled eggs (Colman & Burch 1977).

Economic Significance

In Australia, snails are of economic significance primarily as agricultural pests and carriers of disease. Their importance as a food item is minor in comparison with European countries (see also Chapter 1).

Most of the introduced snails and slugs feed on living plants and are pests either because they directly feed on crop seedlings and fruit, or because they can cause contamination to produce. Native species, however, are generally not regarded as pests as they are largely detritivores or fungivores.

Perhaps the most significant pulmonate pest species is the giant African snail, *Achatina fulica* (Fig. 17.21). A varied dietary menu, consisting of about 500 plant species, coupled with large size and voracious appetite, makes this species potentially the most dangerous for agriculturally based countries. It is present in Papua New Guinea and several other Pacific and South-East Asian countries. *Achatina fulica* was first recorded from Australia in the early 1970s. Fortunately, the single outbreak (Gordonvale, north-eastern Queensland) was successfully eradicated (Colman 1977).

Many introduced helicids and limacoidean slugs are pests of garden vegetables. The Asian snail, *Bradybaena similaris* (Fig. 17.22A), has become a pest in cucurbit crops in the Brisbane area where it feeds on young seedlings and causes faecal contamination of produce. In South Australia, the presence of the European helicid, *Cernuella virgata*, in wheat crops at harvest raises the water content of grain samples and reduces the monetary return to growers (Smith & Kershaw 1979); its control



Figure 17.21 A native of East Africa, the giant African snail, *Achatina fulica*, is widely regarded as the world's most significant land snail pest. The one recorded infestation in Australia was eradicated. (After photograph from Watson 1985)

[C. Eadie]

17. PULMONATA

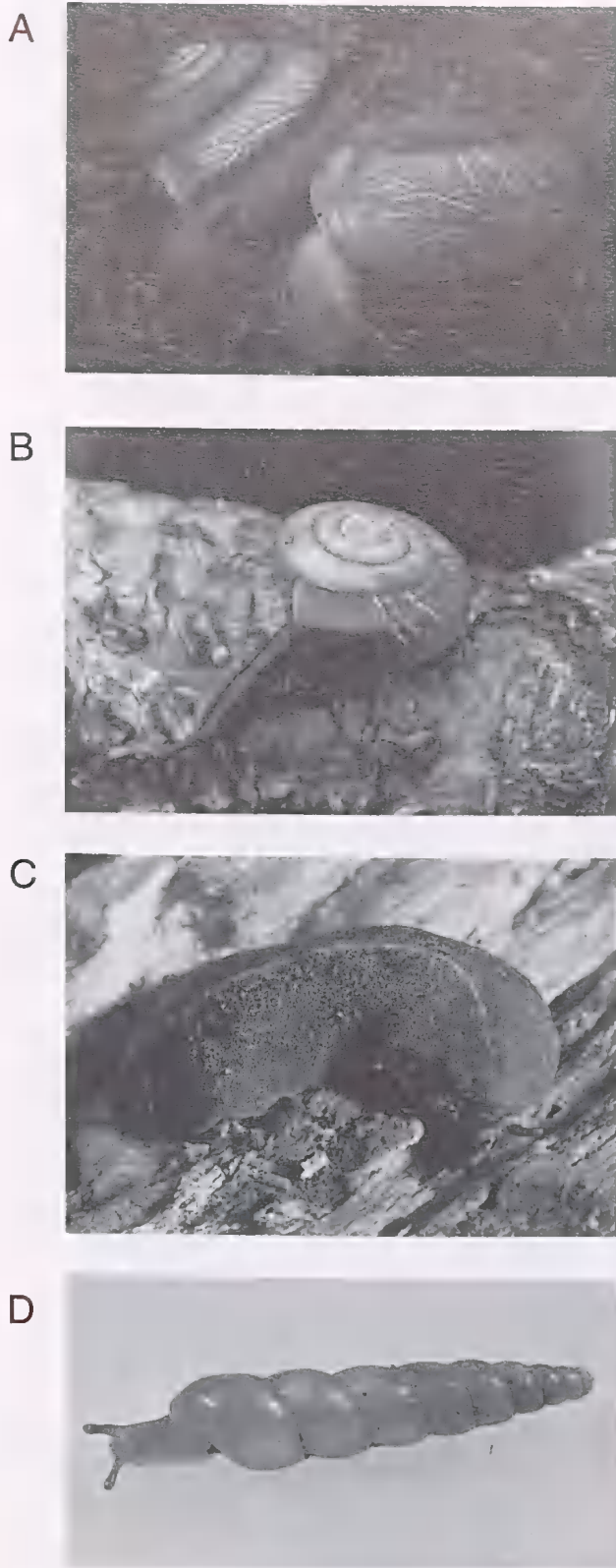


Figure 17.22 Pulmonates introduced to Australia. A, the Asian snail *Bradybaena similaris* (Bradybaenidae), animals from Brisbane; banded and unbanded forms. B, *Zonitoides arboreus* (Zonitidae), the orchid snail introduced from North America is a pest on orchid roots. C, *Laevicaulis alte* (Veronicellidae), is found in northern Australia. D, *Subulina octona* (Subulinidae), originally from tropical America, but now circumtropical, is a detritus-feeder which lives in coastal and adjacent areas of northern, eastern and south-eastern Australia. [Queensland Museum]

has become a major economic issue (Baker, G.H. 1986). The orchid snail, *Zonitoides arboreus* (Fig. 17.22B), which is established in eastern Australia, is a pest of orchid roots and seedlings and comes from the United States of America (Godan 1983). Some introduced European species, for example *Oxychilus* species and *Testacella haliotideae*, are carnivorous and can be beneficial by preying on introduced vegetarian snail species.

Snails are important vectors for human and stock diseases (Malek & Cheng 1974; Godan 1983) but fortunately few of the native species have been implicated as serious problems in this regard (Table 1.3). An exception is the native freshwater snail, *Austropeplea tomentosa*, which acts as an intermediate host for the sheep liver fluke, *Fasciola hepatica* (Boray & McMichael 1961; Boray 1964, 1969). The species ranges widely in eastern Australia, from Tasmania to Queensland (Boray 1964). The same snail species has been implicated in schistosome dermatitis (swimmers itch) caused by *Cercaria longicauda* in New Zealand (Featherston, Weeks & Featherston 1988). A similar dermatitis in northern Queensland involves *Austropeplea lessoni* from freshwaters as a secondary host (Blair & Islam 1983). A more important vector for liver fluke, the introduced *Lymnaea columella*, is now well established in New South Wales (Ponder 1975), and Victoria, Tasmania and Western Australia.

Schistosomiasis (bilharzia), a debilitating disease of humans in Asia and Africa, has the potential to be introduced through the importation of exotic freshwater snails. Some local species of the family Planorbidae may also be potential secondary hosts of this tropical parasite. However, a combination of high hygiene standards and low population density around most of Australia's tropical waterways probably mitigates against the disease becoming a serious and widespread problem among humans in Australia.

Meningoencephalic angiostrongylosis, a parasitic disease of man caused by the rat lung-worm, *Angiostrongylus cantonensis*, has been introduced to Queensland. The introduced slugs and snails, *Laevicaulis alte* (Fig. 17.22C), *Vaginulus plebeius*, *Bradybaena similaris* (Fig. 17.22A), *Subulina octona* (Fig. 17.22D) and probably many other pulmonates are secondary hosts for this parasite which has caused death in dogs and infects humans (Malek & Cheng 1974; Bishop 1977).

Australian culture has yet to accept 'escargot' as a part of its diet. Hence snail farming is not a major industry as it is in parts of Europe. Nevertheless, small scale operations, utilising the introduced garden snail, *Helix aspersa*, have been established in Victoria and New South Wales to supply a limited restaurant trade.

BIOGEOGRAPHY

The basic survey work needed to provide distributional data on most Australian pulmonate species has yet to be done. Checklists of the non-marine fauna were compiled by Iredale (1937a, 1937b, 1938, 1943a, 1944a, 1945) and Smith (1992) but an accurate estimate of the total number of non-marine pulmonate species is not yet possible. Detailed work on the semi-arid zone camaenids of central Australia, Western Australia and South Australia has increased the known number of species in that region from about 100 to over 350 species (Solem 1992). Stanisic (1990) revised 50 charopid species from Queensland and New South Wales, 27 of which were new, from an area traditionally regarded as having a low diversity for the family. A total fauna of over 1200 terrestrial species does not seem unrealistic.

Australia has comparatively few marine and freshwater pulmonates. McMichael & Iredale (1959) and McMichael (1967) presented overviews of the relationships of the freshwater species but without the basis of revisionary studies. Previously Hubendick (1951) had allied the Australian lymnaeids with South-East Asian stock. Walker (1984, 1988) completed a detailed revision of the non-planispiral planorbid genera and concluded that most (*Glyptophysa*, *Ancylastrum* species) are remnants of a Gondwanan fauna, but that at least one (*Amerianna*) arose in the Papua New Guinean-northern Australian region. Brown (1981) considered that the Australian planispiral planorbids are part of more widespread extralimital groups. Australian ancylids show morphological similarities to New Zealand species and are congeneric with species in New Caledonia, Hawaii, the Neotropics and the West Indies (Hubendick 1967).

The bulk of Australian pulmonates are land snails and their distribution over the continent is not homogeneous. Along the east coast (from the Torres Strait Islands to Tasmania) species diversity is high in the rainforests. The main reason for this is that rainforests are now, and have been in the past, important refugia for land snails (Stanisic 1990). The fact the rainforest has persisted and diversified in the face of post-Miocene aridity phases has enabled moisture dependent snails to develop complex sympatric communities in some areas, such as the Border Ranges of southern Queensland and northern New South Wales where more than 60 species occur with 30 to 40 species living at individual sites (J. Stanisic personal observations).

The drier rainforests (vine thickets and vine forests) of south-eastern Queensland, also support around 40 species per site. Mosaic diversity, in which the total faunal complement of an area consists of species clusters confined to particular plant communities has been noted in the tropical rainforests of northern Queensland. The high mountains of this region, such as Mount Bellenden Ker (Fig. 1.102B) and Mount Bartle Frere, have altitudinally segregated rainforest communities. The lowlands and foothills have typically tropical to subtropical vegetation, whereas the mountain summits (above 1000 m) are basically temperate in aspect. These upland environments are refuges for snail species not found at the lower levels (Stanisic 1987, 1990). Of a total of 45 species (from various families) recorded from Mount Bellenden Ker by Stanisic (1982), 14 were confined to the uppermost 500 m.

Development of high land snail diversity has not only involved sympatric communities in regions of high relative moisture. Limestone outcrops, with their ability to trap moisture and with an abundant supply of calcium, have been able to support island-like snail communities in a sea of snail-depauperate countryside. Solem (1988a, 1991) cites the extraordinary example of 28, mainly allopatric, camaenid land snail species from 52 km of limestone hills (Ningbing Ranges and Jeremiah Hills; Fig. 1.103) in the north-eastern Kimberley. The limestones of the Chillagoe–Palmerville area and the Rockhampton region of Queensland, and the many outcrops of the Great Dividing Range in New South Wales maintain diverse sympatric communities. The species complement comprises widespread, dry-adapted forms as well as a significant endemic component which displays relationships with the nearby rainforest fauna (Stanisic 1990).

In each of the above situations, the mechanisms of community evolution have been different. In the rainforests, local, short-term, climate-related barriers and subsequent dispersal in more favourable periods have led to allopatric speciation and the development of sympatric species pairs in some cases (Stanisic 1990). In the Kimberley, radiation into a region devoid of snail competitors, and with flood-assisted, seasonal dispersal, is considered to be the underlying mechanism (Solem 1985b).

At the regional level considerable attention has been paid to endemism levels, resulting in the development of the regional faunal concept. Iredale (1937a) applied the concept to land snails and divided the continent into a number of faunal areas and regions characterised by particular land snail taxa which in turn inferred relationships with extralimital snail faunas: the faunal regions have been modified by McMichael & Iredale (1959) and Smith & Kershaw (1979) (see Fig. 1.90 and pp. 80–82). Hence in the north-east, the Solanderian Region is characterised by the papuinid tree snails, larger camaenids, and several neritopsines and caenogastropods which give it a distinctly Papua New Guinean character. In the south-east, the southern part of the Peronian Region is dominated by charopids, punctids and rhytidids thus implying a New Zealand connection. However, this approach provides very little information on the multiple origins of the snail fauna and the different underlying causes of diversity in a particular area. Stanisic (1994b) proposed a system of smaller subfaunal units based on coincidence of species ranges.

Regional data currently available on the terrestrial pulmonates are shown to be inadequate when tested by rigorous survey work. Smith (1984) presented a contemporary summary, but for data

other than on the south-east of the continent (Smith & Kershaw 1979, 1981), he relied on incomplete check-lists. An exception to this is the work on Kimberley and northern Australian land snails by Alan Solem (Solem 1988b, 1991; Solem & McKenzie 1991) which was based on collections from numerous and widespread collecting sites. Solem (1988b) recorded a total of 245 land snail species (including several neritopsines and caenogastropods) for the Kimberley. Most of these were shown to be endemic to the Kimberley: only several had extended ranges (Solem 1988a).

Hypotheses about the origins of the Australian land pulmonate fauna have been proposed, but because of the lack of basic comparative studies, these are largely speculative.

McMichael & Iredale (1959) extended the regional fauna concept and divided pulmonates into southern or Gondwanan and northern or Palaeo-Oriental families, complemented by a small component of endemics. However, the treatment was flawed because of the excessive splitting of single family units. Solem (1959a, 1959b) rationalised the taxonomy and placed a greater emphasis on connections with near Pacific Islands. Bishop (1981) presented an analysis which acknowledged the lack of basic family distribution data in many parts of Australia.

The southern or Gondwanan families (Bruggen 1980) include the Charopidae, Bulimulidae, Rhytididae and Athoracophoridae, and those families of northern origin include the Camaenidae and Helicarionidae. Families that are part of wider world distributions include the Pupillidae, Punctidae, Succineidae and possibly the Megaspiridae. Families endemic to Australia are the Caryodidae, although possibly part of a wider acavoidean Gondwanan pattern, and the Cystopeltidae, which has been variously related to the Helicarionidae (Hedley 1890) and Charopidae (Tillier 1989).

More rigorous biogeographic analysis requires the development of more robust phylogenies for pulmonate families (reviewed by Emberton *et al.* 1990). It is highly probable that current views on the origins of some groups will be modified significantly. Solem (1985b) concluded that the Kimberley camaenids represent a post-Miocene colonisation from the Indonesian–Timor region and considered that the camaenids of eastern Australia derive from a separate wave of immigrants through the Papua New Guinea area. The multiple origins of the family are supported by morphological data (Solem 1992). Similarly the concept of the Charopidae as a homogeneous, temperately diverse Gondwanan family, is in question. Stanisic (1987, 1990) has established the family as a significant faunal unit in the subtropical and tropical regions of eastern Australia and has reported the presence of a previously unrecorded Rotadiscinae which has North American connections.

Hence, although the origins and affinities of the Australian pulmonates are probably diverse, the validity of such hypotheses has yet to be tested rigorously in most cases.

Lord Howe Island and Norfolk Island have extensive land snail faunas (Iredale 1944a, 1945) which also have yet to be studied critically. The Lord Howe Island species show some connections with Australia, New Zealand and New Caledonia through genera such as *Palaina*, *Placostylus* (Fig. 17.23) and *Hedleyoconcha*. However, the Norfolk Island fauna includes a large number of helicarionids which bear superficial resemblance to Pacific Island species.

Fossil Record

The earliest known land snails occur in the Palaeozoic (Upper Carboniferous or Pennsylvanian) of Europe and North America and include four families (two orders) of stylommatophoran pulmonates (Solem & Yochelson 1979). In contrast, the earliest record of the Basommatophora is from the late Jurassic. The first terrestrial basommatophoran was the ellobiid genus *Carychium* and the first freshwater ellobiids include *Zptychius*. The oldest known higher limnic Basommatophora (Physidae, Planorbidae and Lymnaeidae) have been found in the late Jurassic Morrison Formation (Solem & Yochelson 1979).



Figure 17.23 *Placostylus bivaricosus* (Bulimulidae), one of the endemic snails on Lord Howe Island. [I. Hutton]

The non-Australian pulmonate fossil record is relatively extensive (Zilch 1959). In comparison the Australian non-marine fossil record is poor. Of the 17 stylommatophoran families with Australian endemic representatives, only three have a Southern Hemisphere origin in the fossil record (see Table 17.3). Solem (1979a) summarised the first appearance of land snails in the fossil record and showed that 43 out of 60 pulmonate families have a known fossil record (Table 17.3). Most make their first appearance between the Cretaceous and Eocene and most of the known radiations occur in the Northern Hemisphere where there are better known fossil deposits.

In general, Australian records of pulmonate gastropod fossils are Late Tertiary or Quaternary in age and there has been no attempt to produce a detailed taxonomic analysis of the species which have been found. Generic and familial placements have been made on the basis of gross shell features rather than detailed analysis and any phyletic or ecological inferences which have been made are largely speculative. This problem is exacerbated by the incomplete knowledge of the extant taxa. Even the earliest Australian land snail fossil records (Sowerby in Strzelecki 1845) are still somewhat enigmatic. '*Bulinus gunni*' has been tentatively assigned to *Bothriembryon* (McMichael 1968; Ludbrook 1980) but the relationships of '*Helix tasmaniensis*' are still in doubt; sculptural features (fine arcuate radials and spiral cords) led to an uncertain association of this species with the Rhytididae (Harris 1897).

A suite of species were subsequently described from yellow limestone (travertine) beds, probably of Pleistocene age, at Geilston Bay, Tasmania (Johnston 1880). These included *Helix tasmaniensis*, the extant *Tasmaphena sinclairi* (Rhytididae) and two species of unknown affinity. Pleistocene calcareous beds in the Kent Group, Bass Strait, yielded the keeled '*Helix*' *simsoniana*. This species was initially compared with the extant Tasmanian caryodid *Anoglypta launcestonensis* and the New Zealand *Rhytida greenwoodi*. Kershaw (1988a) considered that it was more probably related to the extant caryodid genus, *Pedinogyra*. Kendrick & Wilson (1975) discussed the relationships of some fossil species of *Bothriembryon* in south-western Australia.

Several fossil pulmonates, from Tertiary limestone rocks of northern Australia, were described by McMichael (1968), among them both freshwater and terrestrial species. The basommatophorans were referred to *Physastra*, *Anisus*, *Gyraulus*, *Isidorella* and *Syrioplanorbis*, all members of the Planorbidae. The last of these is known as a fossil in the Oligocene of Europe and occurs in the Recent of Syria. Land snails included *Bothriembryon praecursoris* (Bulimulidae) and *Meracomelon lloydi* (Camaenidae) but the generic placements were somewhat uncertain.

Ludbrook (1980) documented more fossil land and freshwater pulmonates from Miocene limestone deposits of the Etadunna Formation in northern South Australia. These deposits included species previously described by McMichael (1968). Ludbrook (1978, 1984) also listed a number of Quaternary land snail fossils from South Australia and the western part of the Eucla Basin. All were considered conspecific with extant species. Quaternary fossil land snails have been recorded from limestones at Chillagoe, north-eastern Queensland (Odhner 1917) and Rockhampton, mid-eastern Queensland (Hill, Playford & Woods 1970). Stanisc (1994a) recorded a fossil caryodid from the Eocene deposits in mid-eastern Queensland (Fig. 17.24).

Numerous Quaternary fossils have been recorded from calcarenite ('coral rock') beds on Lord Howe Island (Iredale 1944a) and from Nepean Island, near Norfolk Island (Iredale 1945). The Lord Howe shells were considered to be conspecific with living forms: the Nepean Island forms were distinct from the nearby Norfolk Island species (Iredale 1945).

METHODS OF STUDY

If a study programme requires the collection and subsequent examination of pulmonate specimens, whether simply for identification purposes or more advanced studies, the methods of collection and preservation employed will depend on the objectives of that study program.

Collection of Specimens

Field collectors should be guided by a general knowledge of the ecology and habitat requirements of the species sought. A good general principle to follow is that if dead shells are found live material may not be far away. Unless the animal is needed only empty shells should be collected. When species are taken alive the collector should know if any of them are carnivorous otherwise valuable specimens may be lost by predation in the container—even of the same species, as cannibalism may occur. Live specimens may also eat paper labels if they are confined in containers for long periods.

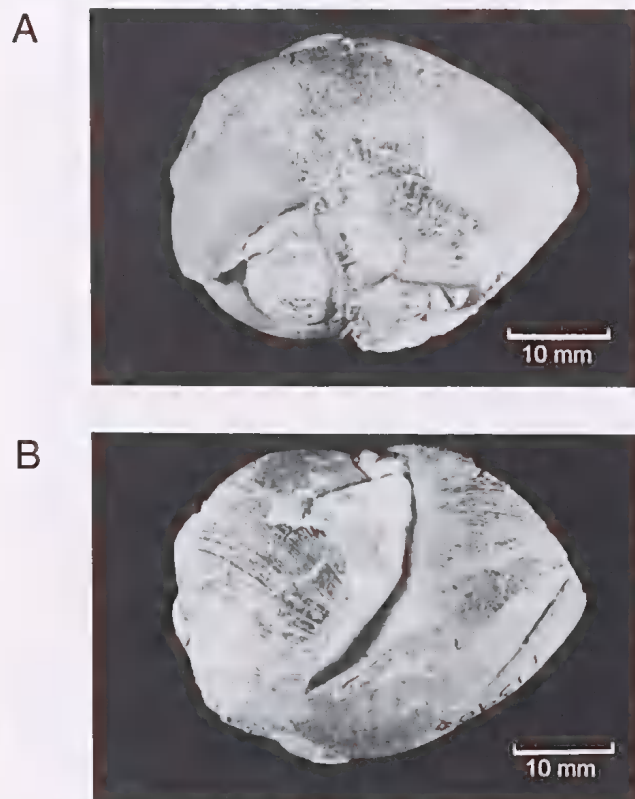


Figure 17.24 *Praecaryodes antiquata* (Caryodidae), a fossil land snail from the Tertiary deposits of mid-eastern Queensland. A, dorsal view; B, ventral view. (From Stanisc 1994a) [Queensland Museum]

Table 17.3 First appearance of native Australian eupulmonatan land snail families in the fossil record. (After Solem 1979a)

Group	Stratigraphic Time	Place
Suborder Stylommatophora		
Infraorder Orthurethra		
Superfamily Achatinelloidea		
Family Achatinellidae	Late Palaeozoic	North America, Europe
Superfamily Pupilloidea		
Family Pupillidae	Late Palaeozoic	North America
Superfamily Partuloidea		
Family Enidae	Late Palaeozoic	North America, Europe
Infraorder Sigmurethra		
Superfamily Achatinoidea		
Family Subulinidae	Palaeocene	Europe
Family Megaspiridae	Cretaceous	Europe
Superfamily Rhytidoidea		
Family Rhytididae	Pliocene	New Zealand
Superfamily Acavoidea		
Family Caryodidae	Eocene	Australia
Superfamily Bulimuloidea		
Family Bulimulidae	Eocene	South America
Superfamily Arionoidea		
Family Punctidae	Oligocene	Europe
Family Charopidae	Miocene	Micronesia
Family Helicodiscidae	Pleistocene	North America
Superfamily Succineoidea		
Family Succineidae	Palaeocene	Europe
Family Athoracophoridae	none	
Superfamily Limacoidea		
Family Helicarionidae	Lower Cretaceous	Europe
Family Cystopeltidae	none	
Family Trochomorphidae	none	
Superfamily Camaenoidea		
Family Camaenidae	Cretaceous	North America

All collections should be accompanied by information about where, when and by whom the specimens were collected. They should also include some note about the type of habitat in which the animals were found. This constitutes the minimum information necessary to accompany each collection in order to make the material of any use for subsequent study and reference. A collector should avoid collecting in any local, state or national parks or reserves. If collecting in such localities is necessary, collecting permits should be obtained as required and only the number of specimens needed for the project should be taken. Once the study has been completed the material should be lodged in a natural history museum.

Collectors of terrestrial species should be aware that different environmental conditions, such as climate can grossly affect the ‘visibility or findability’ of a population. For example, many specimens of the native slug, *Cystopelta purpura*, can be seen on the trunks of the snow gums in the Central Divide of Victoria on cool wet days when the cloud is low and everything is moist/wet. Even an experienced collector looking in the same habitat on a hot, dry, clear day would fail to find any specimens. Many

terrestrial species are active in cool moist conditions, but others are only active in those conditions at night; it is therefore more convenient and pleasant for the collector to seek the animals in their places of shelter under logs, bark or rocks or in leaf litter. The most efficient way to collect the small litter-dwelling species is to collect a quantity of leaf litter and search it at leisure later using a microscope. This can be made semi-quantitative by collecting a standard amount of litter from each sample site.

Many aquatic species may be difficult to find by eye because of silt-laden water or dense vegetation. Hand nets or fine sieves can be used to strain out the larger species from mud and weed and small species can be efficiently collected by washing out weed or dead leaves into a bowl or bucket. The residue can be kept, if necessary, for microscopic examination. Deeper waters can be sampled by means of a small dredge or grab.

Marine pulmonates are collected using methods described in Chapter 1.

Transport of Live Material

Specimens are usually collected alive into small field vials and transported in these pending further treatment. However, even a few minutes in a small sealed tube in hot conditions can kill or seriously distress most species.

If specimens are to be kept alive for long periods, sent through the post or freighted over long distances, special precautions should be taken. It should be remembered that Australia and many overseas countries require permits for the import or export of live specimens. These permits can take time to obtain so the collector should, if possible, obtain the necessary documents before the material is collected to give the molluscs the best chance of survival as they may have to be held in transit while permits are obtained. Live specimens are best transported in moist, soft, non-living material such as dead leaves or damp (but not wet) tissue inside a sealed, inflated plastic bag. This in turn should be packed in soft packing inside a rigid box. Live plant material, such as grass or green leaves, should not be used as this respire in the container and depletes the available oxygen. Aquatic species also travel better in this way rather than in water, which quickly becomes foul, especially if one or two of the animals should die. Food is not usually necessary if the journey is only a day or two. Excessive heating or cooling is a problem and the rigid container and packing should be of some material which will prevent this. If in doubt, the inner plastic bag can be inflated with air to give the specimens a better chance of survival. Material packed in this way can be safely air-freighted to anywhere in the world.

Relaxation of Specimens

All pulmonates should be fully relaxed before killing as this allows better penetration of preservatives and presents the animal in a more convenient condition for dissection. It also allows external features to be examined easily. An evaluation of a number of narcotisation techniques was published by Runham, Isarankura & Smith (1965).

A reliable general technique is to drown the specimens in water with the aid of menthol crystals as a narcotising agent. A vial containing the specimens is filled completely with fresh water, a few small menthol crystals added and the vial sealed to exclude all air and left overnight. Next morning the water can be decanted carefully and fixative added to fix the relaxed specimens. In the case of terrestrial pulmonates, drowning the animals in a jar of freshwater alone, for 12–16 hours, has proved effective (J. Stanisic personal communication). Some slugs produce excessive amounts of very viscous mucus which should be gently removed before the animals are preserved. In an emergency, half a cigarette can be used as a narcotising agent. The tobacco should be removed from the paper, crumbled into the water and used as outlined above for menthol crystals. It is not quite as effective as menthol and has the disadvantage that tiny specimens may become lost in the strands of tobacco.

Preservation and Storage

The method adopted for killing, preservation and storage depends on the purpose for which the specimens have been collected. For use purely in identification of the species or as a general museum specimen, where general dissection is the only requirement, the relaxed animal can be killed by 'fixing' in 90% alcohol. After 24 hours the specimen should be transferred to a fresh solution of 70% alcohol for storage. This treatment gives a general preservation, keeps the internal organs soft, does not attack the shell, and preserves DNA for biochemical studies. Large specimens should be slit or injected to ensure good penetration. If any histological investigations are envisaged for the specimen the animals should be killed by immersion in 10% buffered formalin for six to 12 hours. They should then be washed in fresh, running water for five minutes, rinsed in 70% alcohol for five minutes and stored in fresh 70% alcohol. This method provides good general histological fixation of the tissues as well as preserving the natural colour of the organs and the shell sculpture. It does cause some hardening of the tissues and renders them more brittle in dissection, and tends to destroy DNA.

Other specialised cytological fixatives, such as Bouin's Fixative or Susa, can be used instead of buffered formalin. These preserve the fine structure of the cells and tissues better but are very poor for general dissection and many are acidic and quickly dissolve the shell, and destroy DNA.

The formula for 10% buffered formalin is one part concentrated formaldehyde solution, eight parts water and 5 gm/l of sodium bicarbonate powder. For a double buffered solution, add 6.6 gm of potassium dihydrogen orthophosphate and 31.0 gm of di-sodium hydrogen orthophosphate to 400 ml of concentrated formaldehyde solution, made up to 4 litres with water.

Sodium bicarbonate used with seawater is a good buffer. Ethyl alcohol is recommended for use rather than methyl alcohol as the latter tends to harden tissue.

Culture of Pulmonate Species

Most pulmonate species can be kept alive under artificial conditions for short periods of time. It is, however, a long step from there to either maintaining them in the laboratory for long periods of months or years, or getting them to breed in captivity, rearing several generations. In general, the culture conditions should mimic as closely as possible the natural conditions in which the species are found. The containers and contents should be kept as clean as possible to minimise contamination with such organisms as nematodes and mites.

Many Australian aquatic pulmonate species have been kept and bred in the laboratory (J. Burch & J. Walker personal communication). Conditions are kept favourable for them by providing clean water regularly and feeding with soft plant material such as lettuce. By contrast very few terrestrial species have been bred in captivity. McLauchlan (1951) provided valuable information on which to base further studies. Almost nothing has been published on the basic requirements and details of the life history of most terrestrial species.

Radular Preparation

Examination of the radula is very helpful in the identification of the family and generic placement of many pulmonate species.

The radula of any pulmonate can be extracted either from the buccal mass of large animals or after the shell of small animals is removed. Place buccal mass or entire animal of small species into about 25 ml of a 20% solution of sodium hydroxide in a test tube and heat in a water bath until the specimen has completely broken down – about 10 to 15 minutes or longer if necessary. Decant the material into a glass dish containing twice the volume of cold water, and place it on a dark, obliquely illuminated surface, such as a black tile, against which the radula will be easily seen as a fine silvery ribbon. Transfer the radula carefully with a mounted needle into a watch-glass of clean (preferably distilled) water for preparation for examination.

A Scanning Electron Microscope (SEM) provides by far the most useful and revealing technique of examining the radula. Details of the preparation of pulmonate radulae for examination by this method are given by Solem (1972b). Radulae can also be examined with a light microscope, for which the following method is quick and useful.

Extract the radula and transfer to clean water in a watch-glass. Mix a small amount of the powder stain Lignin Pink into a small quantity of polyvinyl lactophenol to produce a dark red solution. Place two drops of this solution onto one end of a glass microscope slide and transfer the radula into it using a mounted needle (picric acid is also a good stain for this purpose; W.F. Ponder personal communication). Leave the radula in the stain for about five minutes (depending on size). Transfer it gently to a drop of clear polyvinyl lactophenol on the same slide, for one minute. Transfer the stained radula to a fresh drop of clear polyvinyl lactophenol on a clean slide, arrange and cover with a cover-slip.

CLASSIFICATION

The classification of the Pulmonata given below (Table 17.4) incorporates the ordinal categories proposed by Haszprunar & Huber (1990) and the superfamily and family groupings of Solem (1978a) and Hubendick (1978). Tillier (1989) put forward a very different arrangement of families within the Stylommatophora from that of the more traditional system of Solem (1978a). Though Tillier (1989) demonstrated the artificiality of grouping the Sigmurethra on the basis of foot structure – Holopoda, Aulacopoda and Holopodopes – and proposed a division based on kidney shortening (*Brachynephra* versus *Dolichonephra*), this system has yet to achieve universal acceptance. Emberton *et al.* (1990) compared and assessed the levels of discrepancy of five stylommatophoran classifications, and evaluated the use of molecular sequence data in resolving stylommatophoran phylogeny. Adoption of the more traditional approach, which involves no subdivision of the sigmurethran superfamilies, reflects conservatism on the part of the authors.

Nordsieck (1992) further refined the system of Haszprunar & Huber (1990) by including the Systellommatophora in the order Eupulmonata and elevating the Basommatophora to ordinal rank.

Order SYSTELLOMMATOPHORA

Systellommatophorans are slug-like pulmonates which usually lack an internal or external shell or, rarely, have a reduced external shell. The mantle cavity is very reduced or absent. The dorsal mantle forms a notum which covers the head and sides of the body and extends into the hyponotum on the ventral surface (Figs 17.26A, 17.28B). The notum is separated from the hyponotum by a sharp keel or groove, the perinotum. The head usually bears one pair of tentacles. The procerebrum lacks large cells. The lung (pulmonary cavity) is posterior or absent and the pneumostome, anus and excretory pore are located behind the foot. The radula has mainly unicuspidate or bicuspidate teeth. The male gonopore is situated on the right side of the head and the female opening is located in the midline in the pedal groove, posteriorly near the anus or anteriorly near the right oral lappet.

The order is equivalent to the Ditrema, Gymnophila and Gymnomorpha with the addition of the Otinoidea following Tillier & Ponder (1992). Although various authors (Pilsbry 1948; Van Mol 1967, 1974; Solem 1978a; Tillier 1984b) have included the Systellommatophora among the Pulmonata, others, such as Salvini-Plawen (1970), have argued for an intermediate position between the Pulmonata and Opisthobranchia. However, Haszprunar (1988) presented evidence, based on a comparative analysis of the central nervous system, which indicated the monophyletic origin of the true Pulmonata and the Gymnomorpha. This view was further supported by Haszprunar & Huber (1990) and is followed here.

Table 17.4 Classification of the Pulmonata. Only those groups represented in the Australian fauna are included here. Ordinal classification follows Hazprunar & Huber (1990); superfamily and family groupings follow Solem (1978a) and Hubendick (1978). Families represented in Australia by introduced species are marked with an (I) and notes are appended where additional explanation of the classification has been considered necessary.

PULMONATA

Order SYSTELLOMMATOPHORA

Superfamily OTINOIDEA (Note 1)
Family Smeagolidae

Superfamily ONCHIDIOIDEA
Family Onchidiidae

Superfamily RATHOUISEOIDEA
Family Rathouisiidae
Family Veronicellidae (I)

Order BASOMMATOPHORA

Superfamily AMPHIBOLOIDEA
Family Amphibolidae

Superfamily SIPHONARIOIDEA
Family Siphonariidae

Superfamily LYMNAEOIDEA
Family Lymnaeidae (I)
Family Ancyliidae (Note 2)
Family Planorbidae (I; Note 3)
Family Physidae (I)

Superfamily GLACIDORBOIDEA (Note 4)
Family Glacidorbidae

Order EUPULMONATA

Suborder ACTOPHILA

Superfamily ELLOBIOIDEA
Family Ellobiidae

Suborder TRIMUSCULIFORMES

Superfamily TRIMUSCULOIDEA
Family Trimusculidae

Suborder STYLOMMATOPHORA

Infraorder ORTHURETHRA

Superfamily ACHATINELLOIDEA
Family Achatinellidae

Superfamily CIONELLOIDEA
Family Cionellidae (I)

Superfamily PUPILLOIDEA
Family Pupillidae (Note 5)
Family Pleurodiscidae (I)
Family Valloniidae (I)

Superfamily PARTULOIDEA

Family Enidae

Infraorder SIGMURETHRA

Superfamily ACHATINOIDEA

Family Ferrussaciidae (I)
Family Subulinidae
Family Megaspiridae
Family Achatinidae (I; Note 6)

Superfamily STREPTAXOIDEA

Family Streptaxidae (I)

Superfamily RHYTIDOIDEA

Family Rhytididae

Superfamily ACAVOIDEA

Family Caryodidae

Superfamily BULIMULOIDEA

Family Bulimulidae (Note 7)

Superfamily ARIONOIDEA

Family Punctidae
Family Charopidae
Family Helicodiscidae
Family Arionidae (I)

Superfamily LIMACOIDEA

Family Limacidae (I)
Family Milacidae (I; Note 9)
Family Zonitidae (I)
Family Trochomorphidae (Note 10)
Family Helicarionidae
Family Cystopeltidae (Note 8)
Family Testacellidae (I)

Superfamily SUCCINEOIDEA

Family Succineidae
Family Athoracophoridae

Superfamily POLYGYROIDEA

Family Corillidae (Note 11)

Superfamily CAMAENOIDEA

Family Camaenidae

Superfamily HELICOIDEA

Family Helicidae (I)
Family Bradybaenidae (I)

Note 1. The inclusion of the Smeagolidae in the Otinoidea follows the suggestion of Tillier & Ponder (1992).

Note 2. The family Ancyliidae is here kept as a separate entity following Zilch (1959) rather than combining it with Planorbidae in the new family Ancyloplanorbidae as proposed by Hubendick (1978). The name Ancyloplanorbidae is not valid as it is not based on an existing genus name.

Note 3. The status of the family Planorbidae and various subdivisions of the family are in a state of flux at present with work by Walker (1984) and others helping to clarify this difficult group.

Note 4. The superfamily Glacidorboidea and family Glacidorbidae are tentatively placed here as originally suggested by Ponder (1986) pending further assessment of the affinities of the group.

Note 5. The family Pupillidae is used here in the sense of Solem (1978a), to include the families Vertiginidae, Orculidae and Chondrinidae of Zilch (1959), following Smith (1992).

Note 6. The family Achatinidae is listed tentatively as part of the Australian fauna following the 'outbreak' of *Achatina fulica* in North Queensland recorded by Colman (1977). Although this population has now been eradicated, it is almost inevitable that this pest should become established in northern Australia in the near future, if it is not already there unrecorded. It is widely distributed on islands of the South-West Pacific and in New Guinea.

Note 7. Burch's (1976b) suggestion that the family Bulimulidae should be called Orthalicidae was followed by Smith & Kershaw (1979) in their work on the south-eastern Australian fauna. Here, however, the traditional use of the well-known name Bulimulidae is followed, as advocated by Solem (1978a).

Note 8. The omission of the family Cystopeltidae by Solem (1978a) was probably an oversight. The superfamily placement of this family is unsure, and until more work on its relationships has been done it is placed tentatively in the Limacoidea, an arrangement which possibly reflects its relationships.

Note 9. The family Milacidae is listed here separately from Limacidae, following Altena & Smith (1975), rather than as part of it, as treated by Solem (1978a).

Note 10. The family Trochomorphidae is included here as a separate family following Zilch (1950) rather than including it with the Zonitidae following Solem (1978a) and Smith (1992).

Note 11. The family Corillidae has been added to the listing given by Smith (1992) to accommodate *Craterodiscus pricei*, which was referred to this family by Tillier (1989).

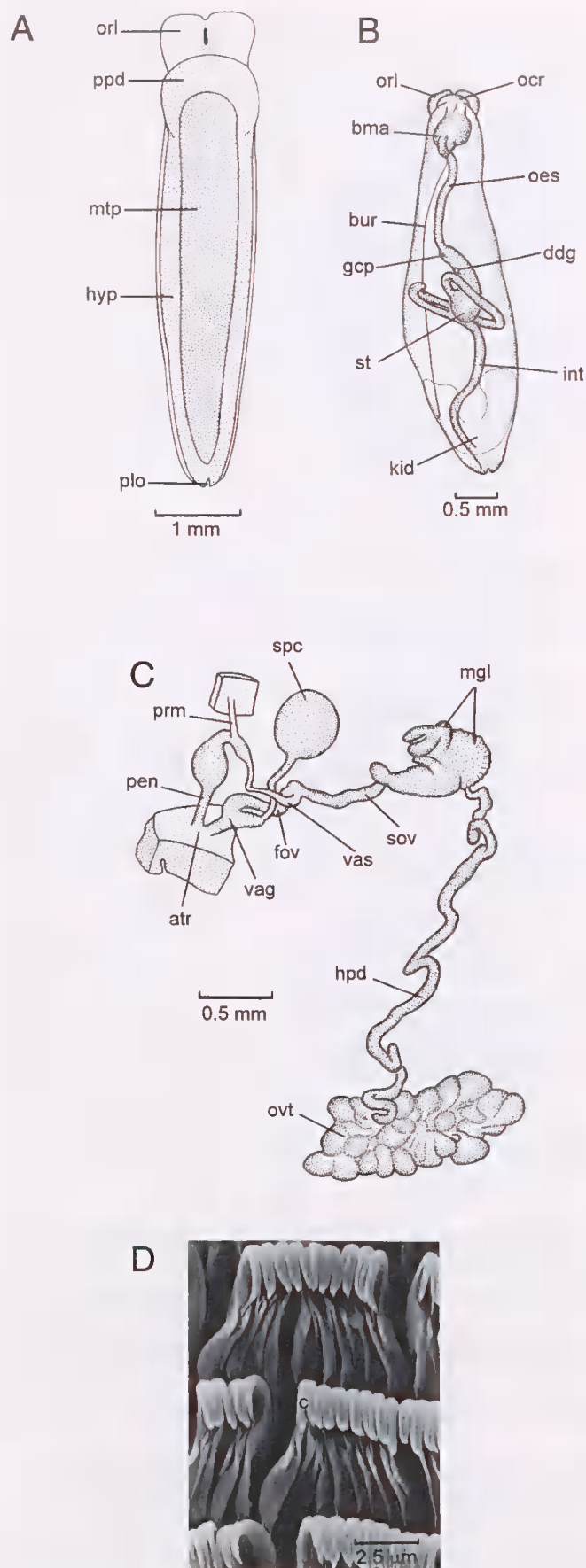


Figure 17.25 Family Smeagolidae. A, B, *Smeagol hilaris*: A, ventral view; B, digestive tract. C, reproductive tract of *Smeagol phillipensis*. D, section of radula of *Smeagol parvulus* showing detail of the central and innermost lateral teeth. atr, atrium; bma, buccal mass; bur, buccal retractor; c, central tooth; ddg, duct of the digestive gland; fov, free oviduct; gcp, gastric crop; hpd, hermaphroditic duct; hyp, hyponotum; int, intestine; kid, kidney; mgl, mucous gland; mtp, metapodium; ocr, ocular ridge; oes, oesophagus; orl, oral lappet; ovt, ovotestis; pen, penis; plo, pulmonary opening; ppd, propodium; prm, penial retractor muscle; sov, spermooviduct; spc, spermatheca; st, stomach; vag, vagina; vas, vas deferens. (A–C, after Tillier & Ponder 1992; D, from Tillier & Ponder 1992) [A–C, D. Wahl]

The Rhodopidae (Riedl 1960; Salvini-Plawen 1970) and the Smeagolidae (Climo 1980) have been tentatively referred to the Gymnomorpha (Tillier 1984b). The Rhodopidae has subsequently been referred to the Opisthobranchia based on the structure of the central nervous system (Haszprunar & Huber 1990). Tillier & Ponder (1992) proposed that Smeagolidae and Otinidae be retained as separate families in the superfamily Otinoidea within the Systellommatophora, on the basis of the synapomorphic occurrence of an ocular ridge and arrangement of the heart and kidney, together with the probably symplesiomorphic foot morphology. This view has been adopted here.

The order comprises three superfamilies, the Onchidioidea, Rathousioidea (= Soleolifera) and Otinoidea, with fewer than 200 species worldwide. All superfamilies are represented in Australia by fewer than 20 species. Members are marine or terrestrial and live from the tropical to temperate regions of Australia. There is no fossil record for this group.

Superfamily OTINOIDEA

Otinoideans are very small marine molluscs with a reduced caplike shell (*Otina*) or with the shell absent. The slug-like forms (*Smeagol*) are elongate with a translucent body and a finely pustulose notum. The pedal sole of the foot is divided into a propodium and a metapodium (Fig. 17.25A). Ocular tentacles are present or absent (*Smeagol*), but an ocular ridge connecting the tentacles or the points corresponding to the tentacles is always present (Tillier & Ponder 1992). The radula has a reduced unicuspidate central tooth, bicuspidate laterals and marginals, and tooth rows aligned transversely. The lung is reduced and opens into a reduced mantle cavity equivalent to the pneumostome of other pulmonates. The kidney is not completely surrounded by lung roof and shares at least one wall with the visceral cavity. There is no conspicuous ureter. The heart is located dorsal to the kidney with the pulmonary vein–aortic axis crossing the kidney. The female gonopore is situated anteriorly on the right side near the male genital opening.

Two families have been included in the superfamily following Tillier & Ponder (1992). The monotypic Otinidae contains an intertidal species from the coasts of Britain and France. Smeagolidae embraces a single genus, with three named species occurring in south-eastern Australia and two in New Zealand. They favour gravel shores.

Family Smeagolidae

Smeagolids lack a shell and are very small to small (3–15 mm long) with an elongate, translucent, white body. The brown digestive gland and yellow to orange gonads are visible through the body wall. The notum appears smooth but is microscopically pustulose and the anterior portion of the pedal sole of the foot is formed into a propodium. The ocular tentacles are absent and there are no pigmented eyes.

A comprehensive review of the family was provided by Tillier & Ponder (1992). A single genus, *Smeagol*, containing five species from Australia and New Zealand, is included. Three species occur in south-eastern Australia from southern New South Wales to Tasmania. Climo (1980) introduced the genus and created a new order for the family. Tillier (1984b) considered that the genus *Smeagol* is a modified otinid and Haszprunar (1985) referred it to the Opisthobranchia. Subsequently, Haszprunar (1988) and Haszprunar & Huber (1990) referred *Smeagol* to the Systellommatophora, based on a study of the central nervous system. Tillier & Ponder (1992) reassessed the relationships of *Smeagol* and *Otina* and concluded that the two genera warranted family level separation pending further study, but recognised their monophyly in a single superfamily.

The ventral surface of the foot comprises a hyponotum (outer pedal rim), an anterior propodium and a posterior metapodium (Fig. 17.25A). The anterior rim of the propodium is cushion-like and adheres to the substratum and the metapodium produces

pulsating waves. When the metapodium moves across the base of the propodium the latter is released and the animal moves forward on the metapodium.

The short, broad radula has more than 100 rows of transversely aligned teeth. The central tooth is reduced and unicuspidate, and the laterals and inner marginals are bicuspidate (Fig. 17.25D). The salivary glands are simple and tubular. The stomach is divided into two chambers – the anterior crop which receives the duct of a single-lobed digestive gland, and the posterior stomach proper (Fig. 17.25B).

The posterior pallial complex opens through a short caudal slit located in the posterior midline at the ventral edge of the notum. The pericardium is located between two branches of the kidney and encloses an anterior ventricle and posterior auricle. The kidney is dorsal to the heart and the pulmonary vein–aortic axis crosses the kidney dorsally. The kidney is U-shaped and opens dorsally into a reduced mantle cavity between the anus and opening of the lung. The lung lies free in the visceral cavity and opens into the right side of the mantle cavity. The anus opens on the left side and faecal strings are extruded from the pulmonary opening as the animals move about (Tillier & Ponder 1992).

Haszprunar & Huber (1990) detailed the central nervous system of *S. manneringi* and showed that the pleural ganglia are closer to the cerebral ganglia than the pedal ganglia and that the parietal and pleural ganglia are either fused or not separated. The visceral ganglion is situated on the right side.

Individuals are hermaphrodites and the openings of the gonopores are fused and located at the limit between the lower side of the oral lappet and the propodium. The hermaphroditic duct is simple, and one albumen gland, two mucous oviducal glands and a spermatheca are present (Fig. 17.25C). There is no prostate gland or bursa copulatrix. Tillier & Ponder (1992) indicated that development may be direct and that the animals reproduce in summer, but no life history study has yet been completed.

All species live in the upper littoral zone at or just below the high tide line. They are found in gravel or pebbles with little or no sand, and are attached to pebbles, stones or rocks in damp areas below the surface.

Tillier & Ponder (1992) postulated that smeagolids have had a very limited dispersal capability and that it is likely that *Smeagol* is Gondwanan in origin. There is no fossil history for the family.

Superfamily ONCHIDIOIDEA

Onchidioideans are medium to large-sized, slug-like marine molluscs that lack a shell. The animals are usually oval with a leathery notum which is smooth, or more usually covered with papillae or tubercles that may contain accessory eyes or branchial plumes. The sole of the large, broad foot (Fig. 17.26C) is truncate in front and tapered behind. The head has a single pair of invaginable and retractile tentacles that bear terminal eyes. The radula bears mainly tricuspidate teeth with the laterals and inner marginals aligned obliquely in a steep-V arrangement. The lung cavity is situated posteriorly and the elongate kidney opens into the pneumostome through a short ureter. The female gonopore is situated posteriorly near the anus.

The superfamily comprises the single family Onchidiidae which is represented in Australia by four genera. Species occur from temperate to tropical regions.

Family Onchidiidae

Members of the Onchidiidae are small to large (10–70 mm long) marine molluscs with no internal or external shell. The notum is smooth, or more usually papillate or tuberculate (Fig. 17.26A, B). Each of the single pair of retractable tentacles bears a terminal eye. The foot is broad and large (Fig. 17.26C) and has fine transverse furrows.

No comprehensive modern review of the family in Australia is available although Bretnall (1919) revised the Australian and near Pacific species, and provided a summary of the early literature. Limited regional summaries of species are provided by MacPherson & Gabriel (1962) and Smith & Kershaw (1979), and Semper (1885) and Hoffman (1928, 1929) included references to Australian species. Britton (1984) presented an overview of world Onchidioidea in which the status and main characters of the family and genera were reviewed and redefined. Based on this revision the family contains 12 genera, among which *Onchidium*, *Platevindex* (= *Oncis*), *Onchidina* and *Onchidella* are represented in the Australian fauna by 13 species (Bretnall 1919). None of these genera is restricted to Australia, but several species are endemic. However, the taxonomic status of some of the species is problematic.

The animals are usually oval, rarely circular in shape and the notum may contain accessory eyes as in *Onchidium verraculatum*. Siliceous spicules or branchial plumes and peripheral repugnatorial glands are present. The large foot is flanked by the hyponotum which is separated from the notum by a perinotal groove, the perinotum (Fig. 17.26C).

The radular teeth are aligned in oblique rows. The central tooth is tricuspidate and the bicuspidate laterals and marginals bear a long spade-like principal cusp and a smaller pointed ectocone (Fig. 17.26D). The jaw consists of numerous palatal plates. Onchidiids graze on mud or rock surfaces, presumably feeding on live algae. The pharynx is large and bulbous and leads to a muscular gizzard which in turn links with a pear-shaped stomach. The digestive gland is three- or four-lobed and the anus is situated in the midline behind the posterior end of the foot sole.

The pallial complex is located posteriorly. The U-shaped kidney lies in the middle of the lung roof and opens into the pneumostome through a short ureter. The lung is used for respiration when the animal is exposed to air. In water, respiratory gas exchange takes place through the skin. The heart is slightly anterior to, and to the right of, the lung and its ventricle lies anteriorly. The anus opens posteriorly in the midline.

In the onchidiid central nervous system, the central commissure is very long, the pleural and parietal ganglia are poorly differentiated and all connectives are short.

Onchidiids are hermaphroditic and male and female genital openings are separate. The albumen gland is bilobed (Awati & Karandikar 1948), there is a short diverticulum on the hermaphroditic duct and a bursa copulatrix is present (Fig. 17.26E). The female gonopore is located at the posterior end of the body near the anus.

The structure of the penis varies from simple to complex. In *Onchidium* the penis is a long muscular tube bearing numerous spiny denticulations and a penial gland. In contrast, *Onchidella* lacks accessory structures. Some species, such as *Platevindex chameleon*, lack denticulations in the penial tube. The male gonopore and penis are situated on the right side of the head near the right tentacle. Eggs are laid in sheet-like masses and hatch as juveniles or as free-swimming veligers. A. Smith & Kenny (1987) reported that *Onchidium damelii* mated from September to June in North Queensland and that egg masses laid in cavities in the buttress roots of mangrove trees hatched about twelve days later as free-swimming veligers. Dakin (1947) studied the natural history of several New South Wales species and A. Smith & Kenny (1987) and Kenny & Smith (1987, 1988) provided data on the development, distribution and behaviour of *Onchidium damelii*. Fretter (1943) provided substantial data on the embryology, development and life history of *Onchidella celtica* in the Northern Hemisphere.

Onchidiids live in the littoral zone, usually in sheltered situations mainly associated with estuaries and mangroves around the coastline of Australia. Onchidiids are principally amphibious although individuals can be found just above high tide level. *Onchidella patelloides* lives in the *Galeolaria* zone of rocky shores in south-eastern Australia (Dakin 1952).

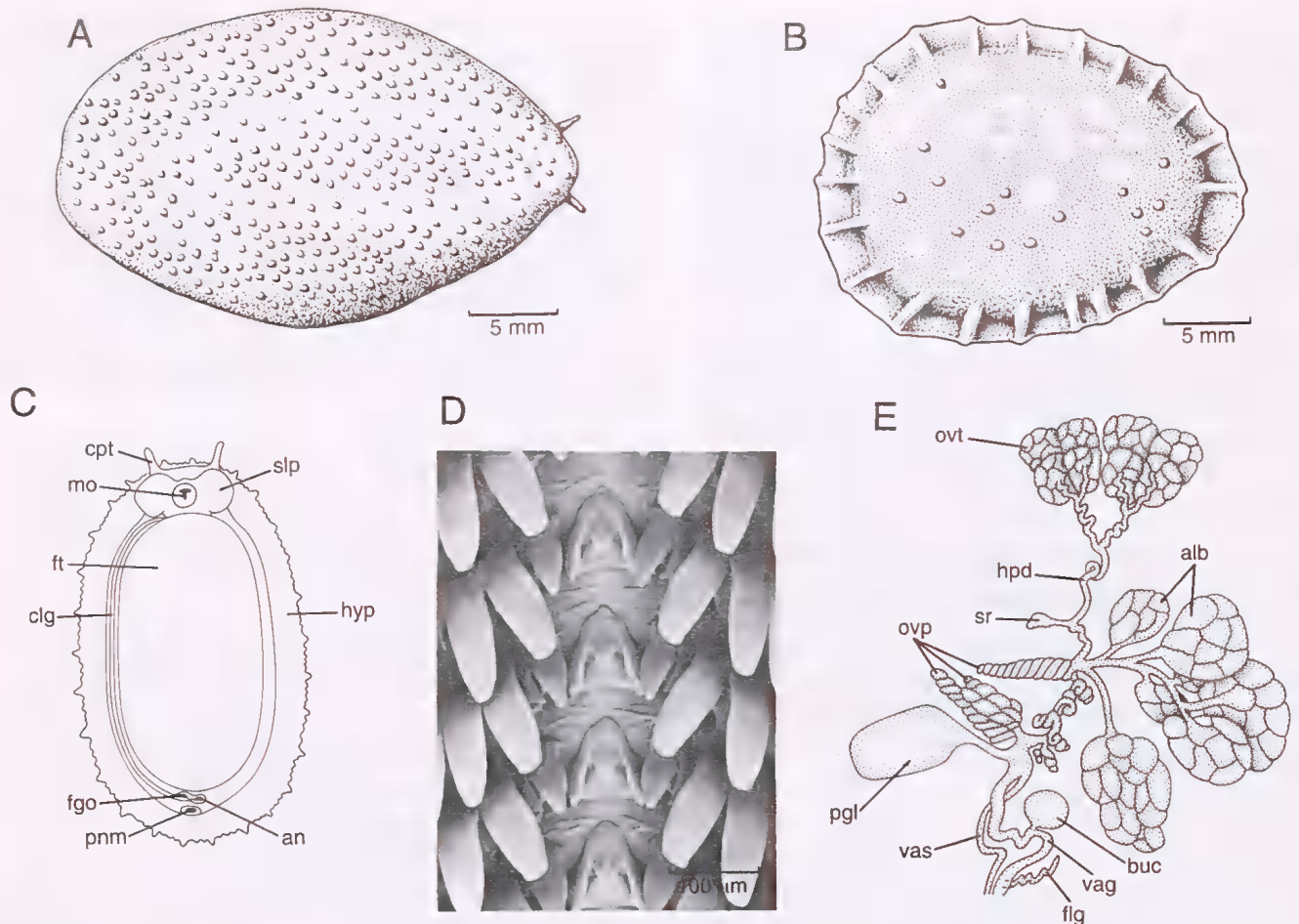


Figure 17.26 Family Onchidiidae. **A**, *Platevindex chameleon*, dorsal view. **B**, *Onchidella patelloides*, dorsal view. **C**, a highly stylised drawing of an onchidiid in ventral view; the shape of the foot is not truly represented (see text). **D**, section of radula of *Onchidium damelii* showing central and innermost lateral teeth. **E**, reproductive system of *Onchidina australis*. alb, albumen gland; an, anus; buc, bursa copulatrix; clg, ciliated groove; cpt, cephalic tentacle; fgo, female gonopore; fig, flagellum; ft, foot; hpd, hermaphroditic duct; hyp, hyponotum; mo, mouth; ovp, oviducal pouches; ovt, ovotestis; pgl, prostate gland; pnm, pneumostome; slp, sensory lappet; sr, seminal receptacle; vag, vagina; vas, vas deferens. (A, B, after Smith & Kershaw 1979; C, after Fretter 1943; D, from Tillier & Ponder 1992; E, after Hoffman 1928)

The family is cosmopolitan in distribution. It occurs from the temperate zones to the tropics, but is most diverse in the oceans of the triangle formed by the Andaman Islands, the Philippines and New Caledonia (Solem 1959b). In Australia, onchidiids live along most coasts, but apparently are absent from south-western Australia.

Superfamily RATHOUSIOIDEA

The Rathousioidea (= Veronicellacea, Soleolifera) is a group of oblong to slender elongate terrestrial slugs with a leathery notum which varies from smooth to weakly tuberculate. The pedal sole of the foot is separated from the hyponotum by a pedal groove (Figs 17.27B, 17.28C). The head has two pairs of tentacles: each of the upper pair bears a terminal eye and is retractile: the lower tentacles are bilobed and tactile. The central tooth of the radula is reduced and unicuspidate or absent, and the radular rows are transverse or disposed in a V-shape. The lung is reduced or absent, the kidney is folded or compressed as a result of limacisation and the kidney pore is contiguous with the renopericardial pore. The ureter leads forward prior to turning posteriorly to the pneumostome (Tillier 1984b). The female gonopore is situated in the pedal groove or hyponotum about midway along the right side of the body.

The superfamily embraces two families – the native Rathousiidae and the introduced Veronicellidae. Both are represented in Australia by species that occur in the tropical and subtropical regions of northern and north-eastern Australia in rainforest and disturbed areas, respectively.

Family Rathousiidae

Rathousiids are slender slugs, usually less than 50 mm in length, and without an internal or external shell (Pl. 31.1). The leathery, weakly pustulose notum is usually keeled midline (Fig. 17.27A). The foot is narrow and delineated from the hyponota by pedal grooves (Fig. 17.27B). The head has two pairs of short tentacles, the upper pair of which bears terminal eyes.

The family includes two genera, *Rathousia* in China, and *Atopos* in India, Indonesia, the Philippines, Papua New Guinea and Australia. Iredale (1938) and Burch (1976b) considered that the Australian species should be included in *Prisma*. Smith (1992) also followed this placement. However, Boss (1982) and Vaught (1989) considered that *Prisma* is either a synonym or subgenus of *Atopos* and this scheme is followed here. Two species are known from eastern Australia. *Atopos australis* (Pl. 31.1) extends from north-eastern New South Wales to northern Queensland and *Atopos prismatica* has been recorded from the Torres Strait (Iredale 1938), Papua New Guinea (Bentham Jutting 1964) and Irian Jaya.

Odhner (1917) presented detailed anatomical data on *Atopos australis* from northern Queensland but no review of the Australian species has been undertaken. De Wilde (1984) detailed the anatomy of a closely related species from Papua New Guinea and discussed the use of the name *Atopos* in preference to *Prisma*.

Animals are variable in external colour, but the variation is not geographically correlated and contrasting colour forms have been collected from the same area (J. Stanisc personal observation). Colour varies from light brown and pale flesh-colour to very dark-brown and almost black, and in paler specimens a fine

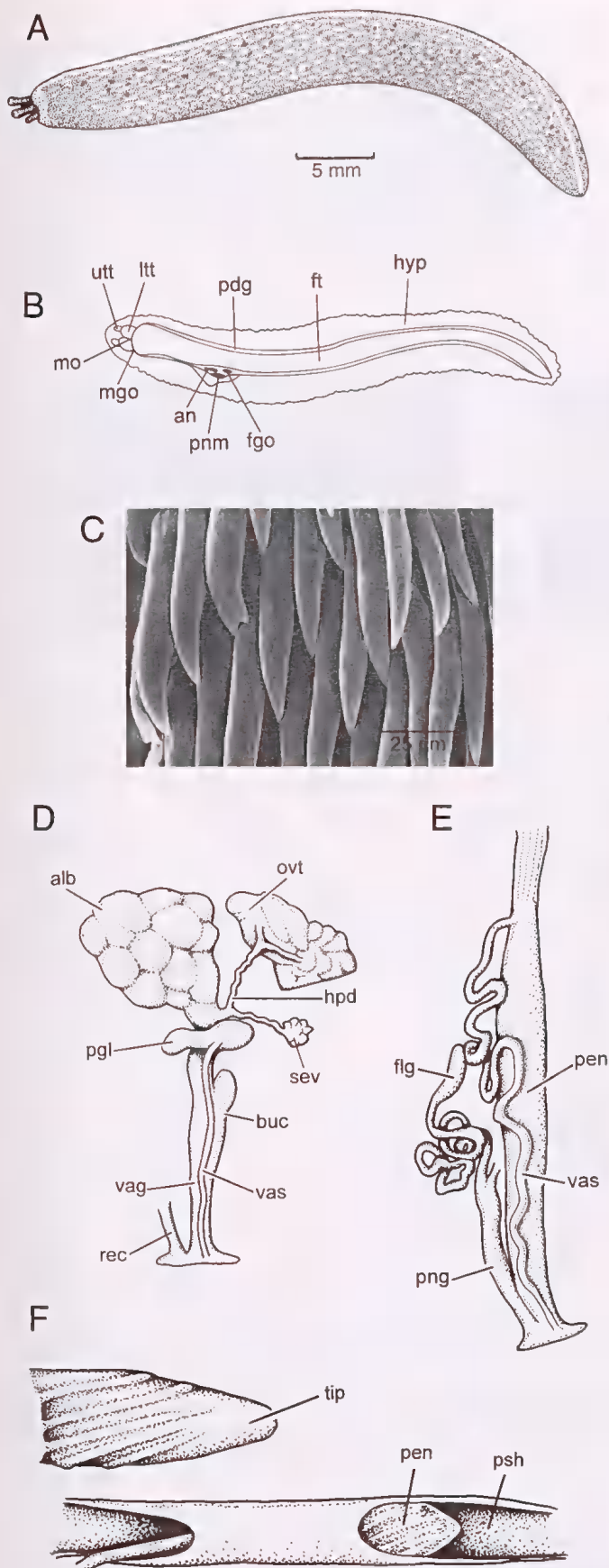


Figure 17.27 Family Rathouisiidae. *Atopos australis*: A, animal, lateral view; B, ventral view; C, portion of radula, showing details of the dagger-like teeth; D, reproductive tract; E, details of male terminal genitalia; F, tip of penis and its placement in the penial sheath. alb, albumen gland; an, anus; buc, bursa copulatrix; fgo, female gonopore; flg, flagellum; ft, foot; hpd, hermaphroditic duct; hyp, hyponotum; ltt, lower tentacle; mgo, location of male gonopore; mo, mouth; ovt, ovotestis; pdg, pedal groove; pen, penis; pgl, prostate gland; png, penial gland; pnm, pneumostome; psh, penial sheath; rec, rectum; sev, seminal vesicle; tip, tip of penis; utt, upper tentacle; vag, vagina; vas, vas deferens. (A, after photograph by Queensland Museum; D–F, after Odhner 1917) [A, C. Eadie; B, D–F, B. Scott; C, Queensland Museum]

reticulate pattern of darker markings is often visible. Animals are not readily seen in the field because of their cryptic colouration and slender body.

The radula of *Atopos australis* consists of V-shaped rows of dagger-like teeth in which the central tooth is absent (Fig. 17.27C). The lateral teeth are unicuspidate and the marginals are similar in shape, but smaller. Some rathouisiid species have a reduced central tooth (Bentham Jutting 1952). No jaw is present (Odhner 1917; Laidlaw 1940). Rathouisiids are largely carnivorous usually feeding on other snails, but fungi and vegetable debris are also included in their diet (Bentham Jutting 1952). The digestive tract is strongly modified for the largely carnivorous diet (Tillier 1984b) in that it is comparatively short and the stomach is long, undifferentiated and sac-like. The digestive gland has no anterior lobe and occupies much of the posterior part of the animal (Odhner 1917; Laidlaw 1940).

The pallial complex is situated in the front half of the body on the right side. A reduced lung opens into the pneumostome, a minute opening located in the pedal groove close to the female gonopore, anus and ureteric opening. The kidney is reduced and located mainly on the left side of the animal. The ureter is short.

The rathouisiid central nervous system is very concentrated: the cerebral commissure is very short and the ganglia of the visceral chain are partly fused. Rathouisiids are hermaphroditic and the genital apparatus is ditrematous and monaulic (Fig. 17.27D–F). A penial gland of unknown function is attached to the base of the penis and a prostate gland is present. The albumen gland is large and the hermaphroditic duct is simple with an attached seminal vesicle (Odhner 1917). A bursa copulatrix is present (Fig. 17.27D).

Laidlaw (1940) provided details of the behaviour of *Rathouisia* species from China, and Loch (1981) discussed some aspects of the ecology of Australian species of *Atopos*. The two Australian species occur in tropical and subtropical rainforest and are found under rotting logs. Smith (1992) reported that they occur in deep litter.

The biogeography of the group will remain unresolved until a revision of the Australian and near Asian species is completed. Comparison of anatomical details provided by Odhner (1917) and De Wilde (1984) indicate a great deal of conchological concordance between Papua New Guinean and Australian species. On the basis of their distribution, it is most probable that the Australian species are post-Miocene immigrants from the Papua New Guinea–Malayan region.

Family Veronicellidae

The Veronicellidae (= Vaginulidae) are a family of medium-sized to large terrestrial slugs, 50–100 mm in length, that do not have an internal or external shell. The animals are oblong and flattened dorso-ventrally (Fig. 17.28A, B). The dorsal surface is covered by a leathery notum and is sharply delineated from the ventral surface by a keeled perinotum. The central foot region is separated from the lateral hyponota by well-defined pedal grooves (Fig. 17.28C). The head has two pairs of tentacles; the upper pair bear terminal eyes.

The family includes about 19 genera found in tropical and subtropical regions of America, Africa, Asia and Oceania. Two introduced species, *Vaginulus plebeius* and *Laevicaulis alte*, have been recorded from Queensland (Bishop 1977) and the Northern Territory (Smith & Dartnall 1976; Smith 1992). These species are circumtropical tramps which were dispersed by 19th and 20th Century commerce (Baker, H.B. 1925; Solem 1959b, 1964a). *Vaginulus plebeius* is native to the West Indies and Brazil and the original range of *Laevicaulis alte* is uncertain (Solem 1964a), although Bishop (1977) suggested that it originated in southern Asia. These species were first recorded in Australia by Simroth (1889) as endemics, but subsequently Grimpe & Hoffman (1925a) placed Simroth's names into synonymy with the

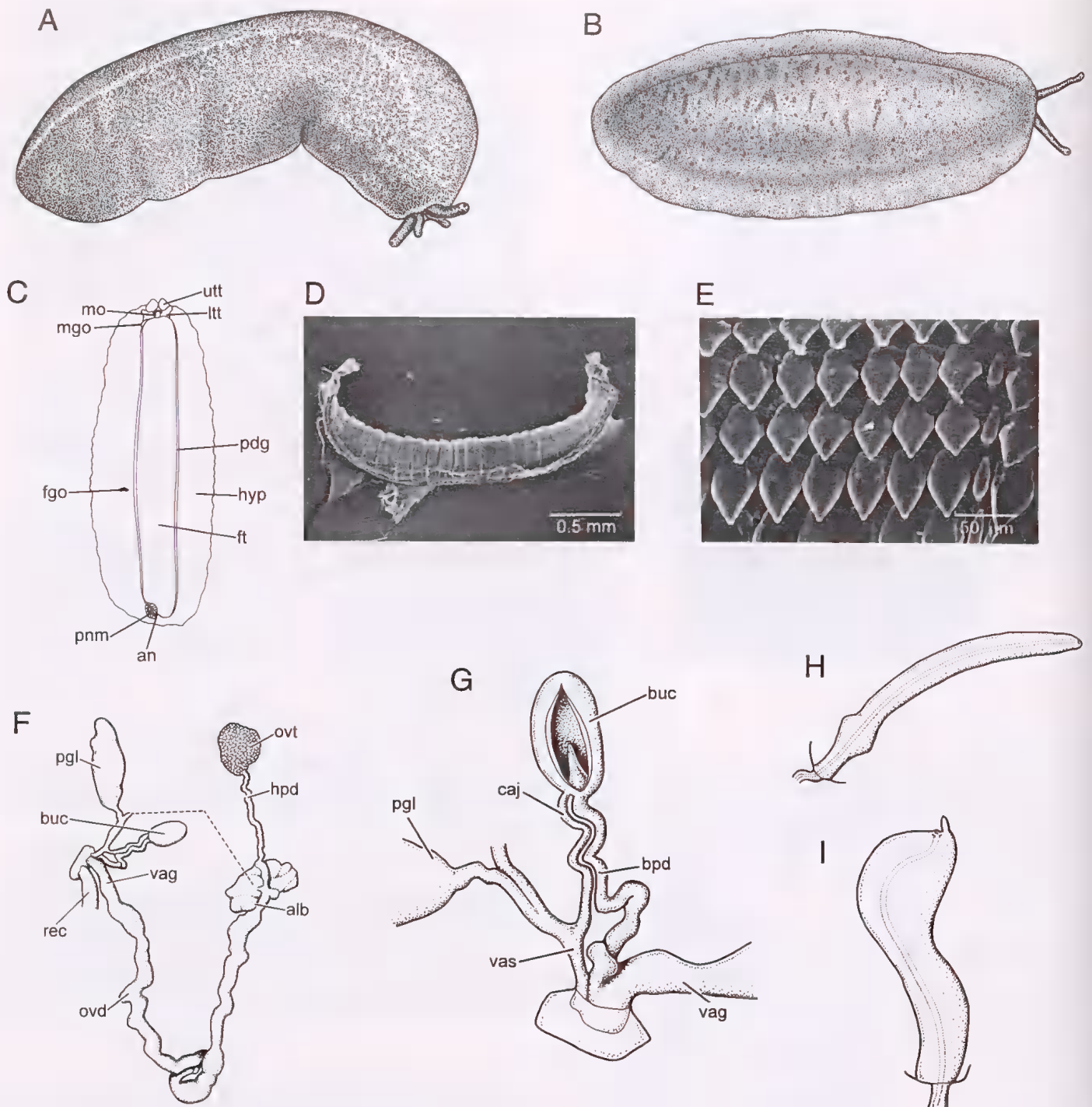


Figure 17.28 Family Veronicellidae. **A**, *Laevicaulis alte*, dorsal view. **B**, *Vaginulus plebeius*, dorsal view. **C**, *Vaginulus plebeius*, ventral view. **D–H**, *Laevicaulis alte*: **D**, jaw; **E**, central and lateral teeth of radula; **F**, reproductive tract, broken line shows point of attachment between the two sites; **G**, details of the terminal genitalia; **H**, penis. **I**, penis of *Vaginulus plebeius*. **alb**, albumen gland; **an**, anus; **bpd**, bursa pedicel; **buc**, bursa copulatrix; **caj**, canalis junctor; **fgo**, female gonopore; **ft**, foot; **hpd**, hermaphroditic duct; **hyp**, hyponotum; **ltt**, lower cephalic tentacle; **mgo**, male gonopore; **mo**, mouth; **ovd**, oviduct; **ovt**, ovotestis; **pdg**, pedal groove; **pgl**, prostate gland; **pnm**, pneumostome; **rec**, rectum; **utt**, upper cephalic tentacle; **vag**, vagina; **vas**, vas deferens. (**A**, **B**, after photograph by Queensland Museum; **F**, **G**, after Bishop 1977; **H**, **I**, after Grimpe & Hoffman 1925a)

widespread species. Forcart (1969) presented additional data on their nomenclatural status and Bishop (1977) provided comprehensive anatomical and distributional data on these two species in Australia.

The jaw is arcuate and composed of numerous vertical plates (Fig. 17.28D; Benthem Jutting 1952). The radula consists of rows of unicuspidate teeth in which the central tooth is smaller and narrower than the laterals which become reduced in size toward the radular margin (Fig. 17.28E). The veronicellid stomach consists of an anterior chamber where the oesophagus, intestine and anterior duct of the digestive gland enter and a posterior chamber which receives the posterior duct of the digestive gland.

The pallial complex is situated within the right body wall. A true lung is absent and the so-called 'lung' of veronicellids is homologous with the mantle cavity of neritopsines and caenogastropods and the pneumostome of pulmonates (Tillier 1984b). The heart is located about midway along the animal and the renopericardial pore is contiguous with the kidney pore. The pneumostome of veronicellids opens posteriorly behind the pedal sole near the anus and the rectum is included in the foot wall on the right side. The kidney is folded and compressed on the right side and the long, S-shaped ureter opens posteriorly near the anus.

The central nervous system has a very long cerebral commissure and a short visceral chain in which the visceral ganglion is slightly more developed on the left than on the right side.

Veronicellids are protandric hermaphrodites and the male and female genital openings are separate (Fig. 17.28C). The female gonopore opens about midway along the right side in the hyponotum and the male gonopore is situated at the anterior end on the right side in the groove between the mouth and the foot.

In veronicellids, a canalis junctor joins the distal portions of the male and female systems, indicating that the diallic system may have been derived from a monaulic ancestor (Fig. 17.28F; Tillier 1984b). An accessory bursa copulatrix may be present or absent. The penial complex consists of a cylindrical, intromittent penial verge and associated stimulator enclosed in a sheath (Fig. 17.28G–I). A prostate gland is present.

In Australia, the two introduced veronicellids occur in subtropical and tropical areas of Queensland and the Northern Territory. They are mainly associated with populated suburban centres although they have also been collected in rural areas where native scrub has been disturbed. They are nocturnal herbivores or omnivores that eat both green and decaying plant material (Solem 1959a) and are usually found under stones, grass, decaying wood and in crevices in the ground. Veronicellids have been implicated as agricultural pests (Bentham Jutting 1952; Solem 1959b; Bishop 1977) and they are also medically significant as vectors of vertebrate nematode infections (Malek & Cheng 1974). The group has no fossil record.

Order BASOMMATOPHORA

Basommatophorans are shell-bearing, terrestrial and aquatic pulmonates in which the eyes are located at the base of a contractile, but not invaginable, pair of tentacles. The shell varies from minute to large, and high-spired to patelliform and planorbiform. It is usually dextral but sinistrality is normal in some families. An operculum is present in adult Amphibolidae and Glacidorbidae. Respiration takes place through a lung, secondary gills and/or epithelium. A true ctenidium is not present although a secondary gill, or pseudobranch, is developed in some species. The mantle cavity is usually closed apart from the pneumostome. The procerebrum contains large cells. Basommatophorans are hermaphroditic, usually with separate genital openings. The anal, renal and genital pores are located near the pneumostome.

The Basommatophora is herein defined following Haszprunar & Huber (1990). Various authors (Van Mol 1967; Tillier 1984b) have separated marine taxa into the Archaeopulmonata as distinct from the freshwater groups or Branchiopulmonata (Morton 1955a). Nordsieck (1992) provided a detailed summary of the many pulmonate classifications developed in the 20th Century and regarded many of the previous groupings that dealt with the Basommatophora to be paraphyletic. Haszprunar & Huber (1990) separated the Basommatophora *sensu stricto* (including the Siphonariidae, Amphibolidae, Chiliniidae, Latiidae and the higher freshwater groups) from the Eupulmonata (including Ellobiidae, Trimusculidae and Stylommatophora) and the Systellommatophora (including *Otina* and the Gymnomorpha). Nordsieck (1992) modified this system and distributed the basommatophoran groups among two orders – the Basommatophora and Eupulmonata. The Glacidorbiidae are tentatively included here following Ponder (1986).

Basommatophorans live either in freshwater or along the edges of the sea. The earliest fossil record is for the ellobiid genus *Carychium*, in the Late Jurassic of Europe. McMichael (1968) recorded several freshwater groups from Australian Tertiary deposits. Representatives of six of the nine recognised families occur in Australia.

Superfamily AMPHIBOLOIDEA

The superfamily Amphiboloidea is represented by a single family of primitive marine pulmonates, the Amphibolidae. These snails have a subglobose shell which is dextrally coiled and has an

operculum. The tentacles are very short with eyes at their bases. The large mantle cavity has strongly vascularised walls and a pneumostome. There is no gill, but an osphradium is present. The broad central tooth of the radula bears five sharp denticles, the two lateral teeth are unicuspidate and tricuspidate, respectively, and the marginals are dagger-shaped. Amphiboloideans are hermaphroditic with diallic (*Salinator*) or monaulic (*Amphibola*) reproductive systems that have separate male and female gonopores. Species of the intertidal genus *Salinator* are the only representatives of the superfamily that occur in Australia.

Family Amphibolidae

These marine pulmonate snails have an operculum in the adult stage. The shell is globose with a depressed spire and an inflated last whorl. The aperture is large and most species have an open umbilicus. Shell height is usually less than 30 mm, and shell sculpture varies from fine to coarse.

Two species are currently recognised in southern Australia – *Salinator solida* and *S. fragilis* (Fig. 17.29A, C; Smith 1992). Woolcott (1945) reviewed features of these two species and separated them on differences in the thin paucispiral opercula (Fig. 17.29B, D). In *Salinator solida*, the inner face has a very conspicuous projecting spiral rib, a feature consistently lacking in *S. fragilis*. The status of the tropical Australian representative is doubtful, but it appears to be like *S. fragilis*.

The shells of *S. solida* and *S. fragilis* have very fine sculpture and are horn-coloured to greyish-yellow with occasional brown spiral lines. The brown colouration appears occasionally as vertical wavy streaks. The radula of *S. cf. fragilis* (Fig. 17.29E) has a broad central tooth with five denticles, a small unicuspidate lateral and a broad tricuspidate lateral, and marginals that are hooked or dagger-shaped (Bentham Jutting 1956). Jaws are absent.

Salinator species are hermaphroditic and male and female genital systems are separate (diallic) (Fig. 17.29F). Details of reproduction are unknown. Amphibolids lay egg strings on the surface of the mud which become covered with a fine coating of silt (Fig. 1.20G; Smith, Black & Shepherd 1989). Healy (1983) presented ultrastructural details of the sperm of *S. fragilis* and *S. solida*. Pilkington & Pilkington (1982, 1984a, 1984b) studied the veliger and settlement and metamorphosis in the New Zealand mud snail, *Amphibola crenata* (Fig. 1.21E).

The large pulmonary cavity has vascularised walls and, in live animals, is filled with water. An osphradium is present but there is no gill. *Salinator* lacks a hypobranchial gland but one is present in *Amphibola*. The kidney is triangular and opens near the respiratory aperture. In *Amphibola*, the gizzard is well developed and the intestine is formed into a spiral. The anus is located on a lobe near the pallial respiratory aperture. The visceral commissure of the nervous system in *Amphibola* is much longer than that of *Salinator* (Fig. 17.29G).

Amphibolids live on estuarine mud flats, sometimes partially buried in the substratum and can withstand brackish water. *Salinator* and *Amphibola* are the only known genera. The former occurs in eastern Asia and Australia, and the latter is found in New Zealand.

Superfamily SIPHONARIOIDEA

Siphonarioideans are marine pulmonates with small to medium-sized, patelliform shells usually with strong radial sculpture (Pl. 31.5). A siphonal groove is located internally on the right side of the shell. This is seen as a ridge externally. A pair of reduced tentacles are present. The mantle cavity is large and open with an osphradium and accessory gill. The radula has a reduced central tooth and numerous denticulate marginal teeth. A jaw is present. Siphonarioideans are hermaphrodites with completely monaulic reproductive systems.

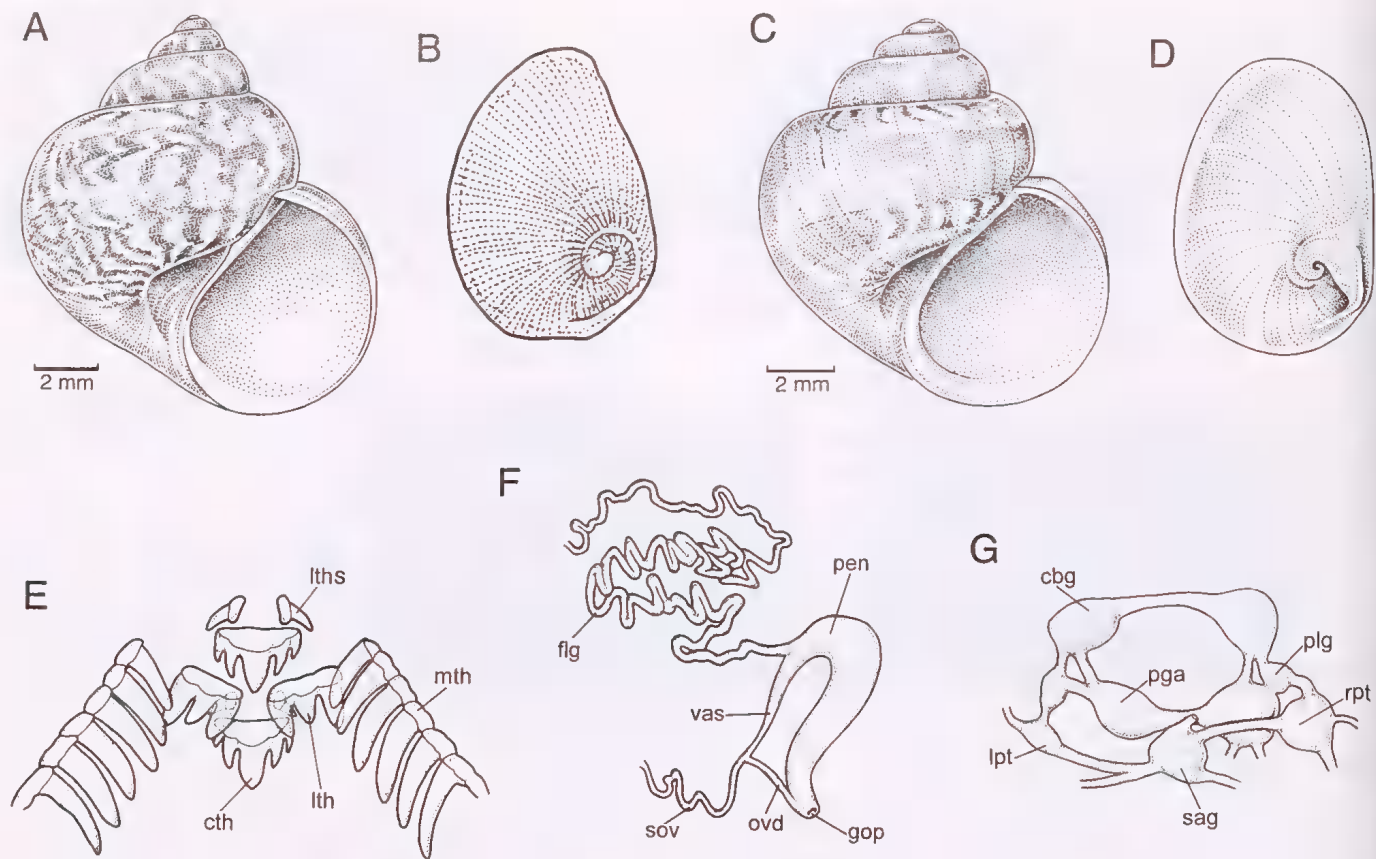


Figure 17.29 Family Amphibolidae. A, B, *Salinator fragilis*: A, shell, apertural view; B, operculum. C, D, *Salinator solida*: C, shell, apertural view; D, operculum. E, *Salinator cf. fragilis*, section of one transverse row of radular teeth plus a central tooth and the small lateral teeth of the next row above shown. F, G, *Salinator fragilis*: F, terminal genitalia; G, principal nerve ganglia. cbg, cerebral ganglion; cth, central tooth; fig, flagellum; gop, gonopore; lpt, left parietal ganglion; lth, lateral tooth; lths, small, unicuspidate lateral tooth; mth, marginal teeth; ovd, oviduct; pen, penis; pga, pleural ganglion; plg, pleural ganglion; rpt, right parietal ganglion; sag, subintestinal abdominal ganglion; sov, spermoviduct; vas, vas deferens. (B, E, after Benthem Jutting 1956; D, after Woolacott 1945; F, G, after Hubendick 1945a) [A, C, D, R. Plant; B, E–G, B. Scott]

The single family, the Siphonariidae, includes about 70 species worldwide (Hubendick 1945b).

Family Siphonariidae

The patelliform shell of siphonariids is thin, ovate and asymmetrical with a subcentral, and often eroded, apex (Fig. 17.30A–E). Shell sculpture consists of irregularly spaced radial ribs and growth striae. The radial ribs are often white with chocolate coloured interstices. The shell length is usually less than 50 mm. The interior of the shell is polished and often coloured with purplish-brown suffusions. The siphonal groove is usually distinct and interrupts the horseshoe-shaped pedal muscle scar on the right side.

Tenison Woods (1879), McAlpine (1952) and Hubendick (1954) dealt specifically with Australian siphonariids and provided morphological and distributional data on a number of species. Iredale (1940a) created eight genera for the eastern Australian siphonariids based on small conchological differences between species. These taxa have not found general acceptance in subsequent literature and are considered to be synonymous with *Siphonaria*. The studies of Jenkins (1981, 1983, 1984) provided significant data on several species from southern Australia. However, no comprehensive review of all Australian species has been undertaken. Hubendick (1945b) presented a detailed phylogeny and biogeography of the Siphonariidae together with details of siphonariid anatomy. *Siphonaria* is the principal genus with over 70 species (Hubendick 1945b).

The animal is pale to creamy-yellow in colour with variable grey-black markings. Tentacles are absent and the sole of the foot is oval and entire. The large mantle cavity covers most of the

dorsal side of the body and opens on the right (Hubendick 1945b). The kidney is flattened and extends over the base of the mantle cavity near the pericardium and a well-developed secondary gill is situated at the posterior end. Dorsal and ventral ciliated ridges lead posteriorly within the mantle cavity. The jaw consists of numerous tiny rods and is slightly arched. The central teeth of the radula are much smaller than the lateral teeth and have denticulate cutting edges. The bicuspidate inner lateral teeth have a long mesocone and a short pointed ectocone. The outer lateral teeth are basically low tricuspidate with a split mesocone. The marginal teeth are strongly denticulate (Fig. 17.30F, G). *Siphonaria* has a simple stomach with only a reduced gizzard.

Siphonariids are protandric hermaphrodites. A long spermoviduct is present and a single genital pore is situated on the right side behind the head. A penis is lacking but is replaced by an epiphallus gland (Hubendick 1978) which has an attached flagellum (Fig. 17.30H). The sperm is transferred in a long chitinous spermatophore (Fig. 17.30I; Jenkins 1984).

Considerable information is available on the reproductive biology of some Australian species. Mapstone (1978) investigated the spawn and early development of *Siphonaria diemenensis* and *S. baconi*. Creese (1980) studied the reproductive cycles and fecundities of *S. denticulata* and *S. funiculata* (as *S. virgulata*) from the Sydney region, New South Wales. He found that *S. denticulata* lays coiled gelatinous egg ribbons on rocky shores (Fig. 17.30A) and *S. funiculata* lays globular egg masses in the sea. The breeding season of *S. denticulata* extends from November–December to the following April–May and spawning occurs every two weeks in the larger adults. Fecundity rates differed according to locality but were the same for the two species at the same locality, at similar size.

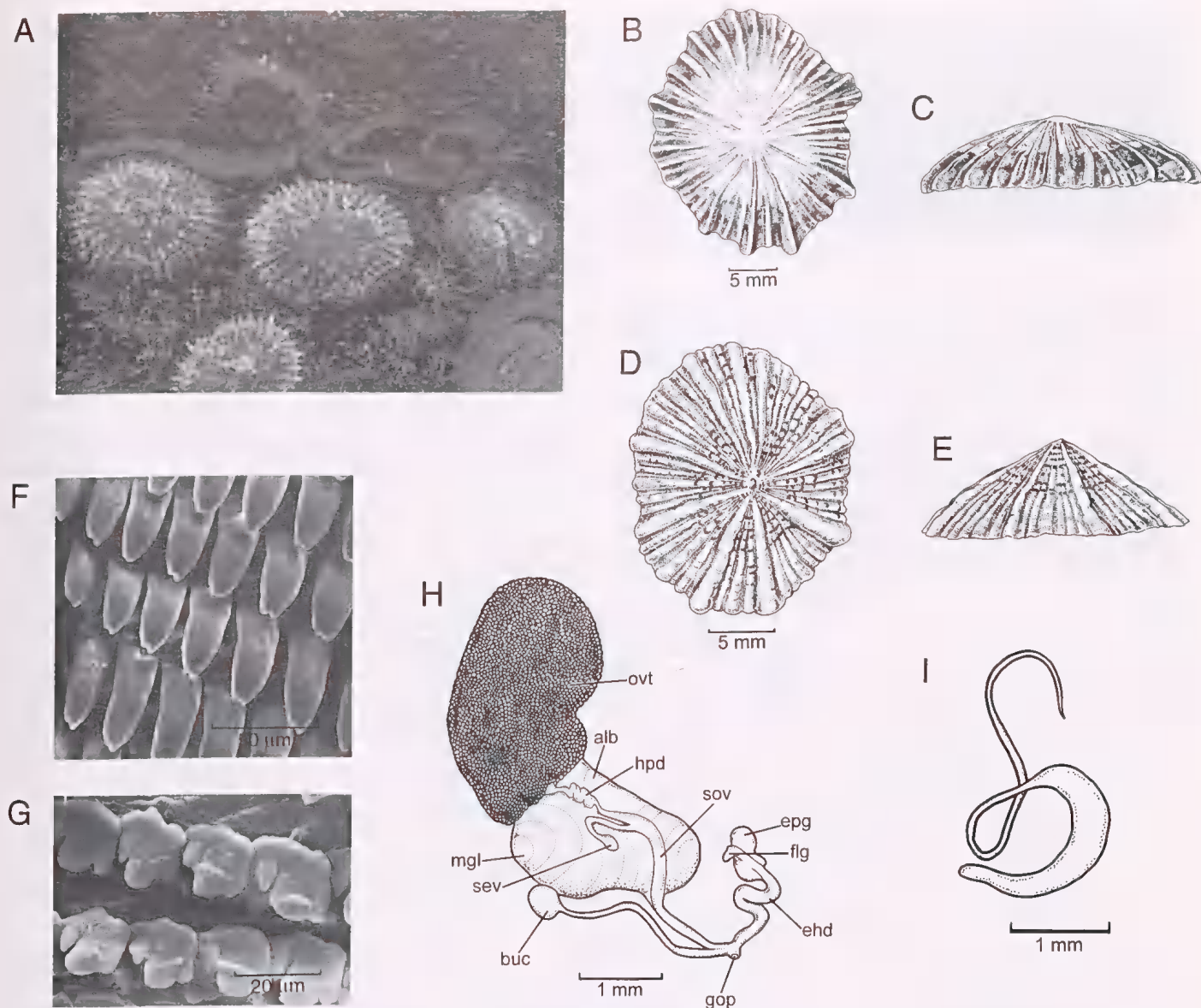


Figure 17.30 Family Siphonariidae. A, *Siphonaria denticulata*, with egg masses, Caloundra, Queensland. B, C, *Siphonaria atra*, shell: B, dorsal view; C, lateral view. D, E, *Siphonaria laciniata*, shell: D, dorsal view; E, lateral view. F, G, *Siphonaria denticulata*, radula: F, central and lateral teeth; G, marginal teeth. H, I, *Siphonaria jeanae*, reproductive anatomy: H, reproductive tract; I, spermatophore. alb, albumen gland; buc, bursa copulatrix; ehg, epiphallus gland; epg, epiphallus gland; flg, flagellum; gop, gonopore; hpd, hermaphroditic duct; mgl, mucous gland; ovt, ovotestis; sev, seminal vesicle; sov, spermoviduct. (H, I, after Jenkins 1984)

[A, L. Newman & A. Flowers; B–E, R. Plant; F, G, Queensland Museum; H, I, B. Scott]

Quinn (1983) showed that *S. tasmanica* produces pelagic egg masses similar to *S. funiculata*. Both these species live higher on the shore than either *S. diemenensis* or *S. denticulata* and this behaviour may be an adaptation related to the greater chance of desiccation higher on the shore (Quinn 1983). Simpson & Harrington (1985) studied the egg masses of *Kerguelenella lateralis* from Macquarie Island and found that this species had non-pelagic larvae.

Siphonariids are marine and live in shallow tidal areas in Subantarctic, temperate and tropical regions of the world, with the exception of the North Atlantic. Most species can withstand exposure to air for long periods.

Superfamily LYMNAEOIDEA

Freshwater pulmonates of the Lymnaeoidea have a variably shaped, thin shell which may be sinistral or dextral, and lack an operculum. The aperture is generally large and usually lacks denticulations or lamellae. The columella may be slightly twisted. The tentacles are either filiform and circular or triangular and flattened. The mantle cavity is closed and vascularised. A pseudobranch may be present or absent.

The radula typically consists of a central tooth which is unicuspidate or variously denticulate, and lateral and marginal teeth which are arranged in straight, transverse rows or are obliquely disposed, sometimes with unusual basal appendages (Physidae).

Lymnaeoideans are hermaphrodites with partially or completely diallic reproductive systems. The gonopores are separate.

The superfamily includes most freshwater pulmonates. Four families occur in Australia—the Lymnaeidae, Ancyliidae, Planorbidae and Physidae. The latter is introduced.

Family Lymnaeidae

The shell whorls of lymnaeids are rounded and the last whorl is usually wide and inflated. The aperture is large and has a fragile peristome. In most species, the shell is high-spired, dextral, rarely sinistral, rimate or with a closed umbilicus. Reduction of the spire and whorl number occur in some species. The shell is usually thin with a weakly developed columellar callus and the sculpture is generally reduced or absent. A colour pattern is lacking (Fig. 17.31A–C).

17. PULMONATA

Iredale (1943a) listed numerous Australian species and introduced several new genera. However, Hubendick (1951) considered the Australian fauna to consist of three species in a single genus *Lymnaea*. Boray & McMichael (1961) reduced this to two species. Inaba (1969) and Smith & Kershaw (1979) considered the Australian and New Zealand species separable under *Austropeplea*. In addition to the endemic species, *Austropeplea lessoni* and *A. tomentosa*, several introduced species have been recorded. Musson (1890) listed *Lymnaea peregra* and *L. stagnalis* and Ponder (1975) added the North American *Pseudosuccinea columella* (see Smith 1992).

The shell is usually smooth or, in *Pseudosuccinea columella*, incised with fine spiral lines. The animal is characterised by a large foot and wide triangular tentacles which are flattened dorso-ventrally. Sensory epithelium also extends posteriorly from the tentacles. The mantle cavity has no pseudobranch or secondary gill.

The central teeth of the radula are unicuspidate or indistinctly and asymmetrically tricuspidate. The lateral teeth are bicuspidate or tricuspidate and there are numerous multicuspidate marginal teeth (Fig. 17.31D). In *Austropeplea lessoni* and *A. tomentosa*, the laterals are tricuspidate. According to Boray & McMichael (1961), the radulae of these two species display a great deal of

variation, but generally the central teeth are unicuspidate with a small accessory cusp; the lateral teeth are usually bidentate with an accessory cusp on the inner edge; and the inner marginal teeth have at least four cusps which become long, slender, and unicuspidate towards the outer margin of each tooth row. The tripartite jaw of lymnaeids has a curved central piece and two lateral pieces.

The digestive system consists of an oesophagus which opens into a thin-walled crop, a well-developed gizzard consisting of two muscular pads, a gastric caecum and a bilobed digestive gland (Fig. 17.31E).

The nervous system is characterised by a short visceral loop. Chiastoneury is absent.

Cross-fertilisation is the general rule, however, self-fertilisation has been reported for the family (Hubendick 1951). The male gonopore opens at the posterior margin of the right tentacle and the female gonopore opens in the neck region on the right side. The penis is enclosed in a sheath with a well-developed praeputium and terminal pore (Fig. 17.31F, G). The prostate gland consists of one or two swellings on the wall of the sperm duct. Eggs are laid in a gelatinous mass.

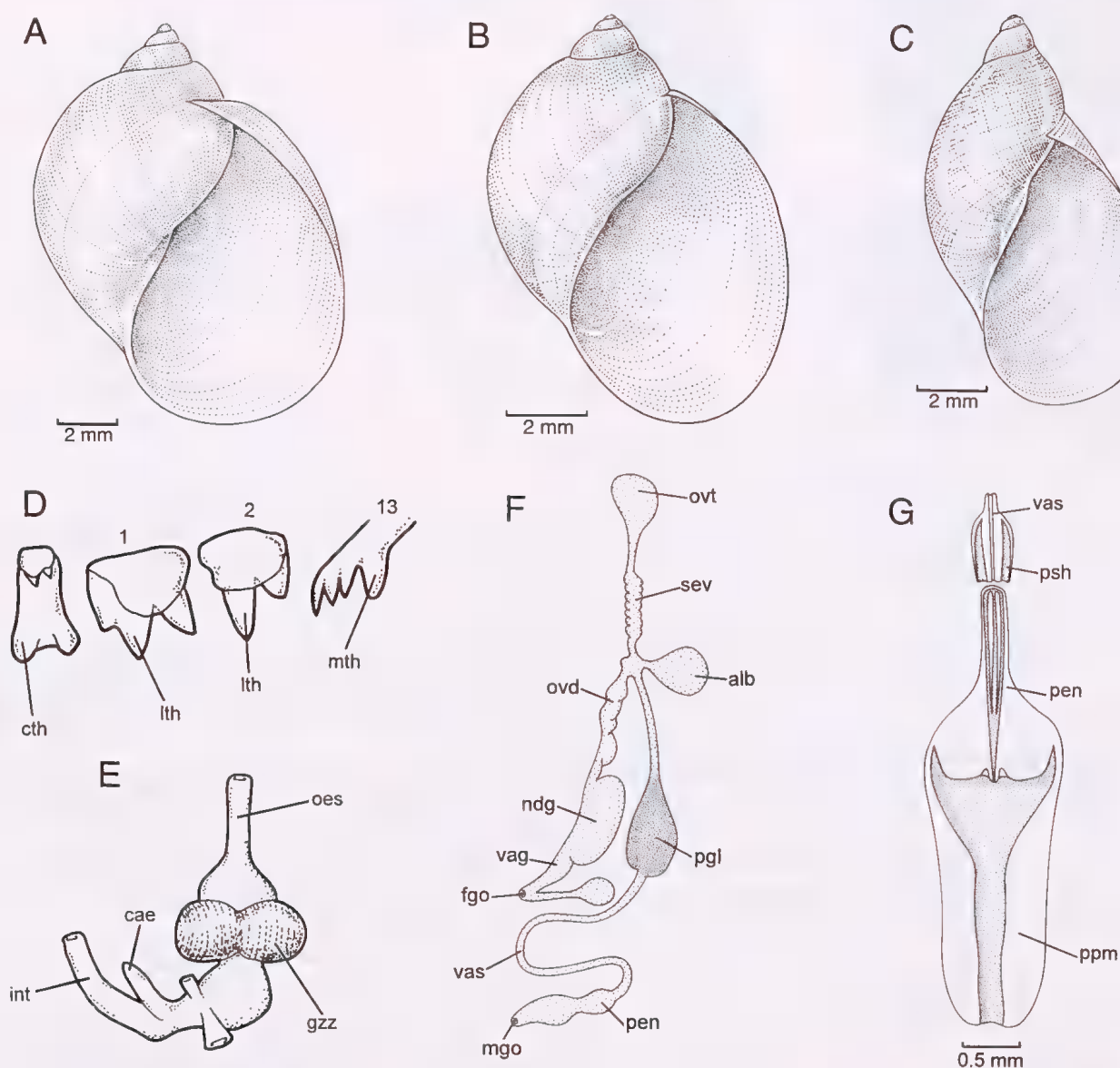


Figure 17.31 Family Lymnaeidae. A–C, shells, apertural view: A, *Austropeplea lessoni*; B, *Austropeplea tomentosa*; C, *Pseudosuccinea columella*. D, *Austropeplea tomentosa*, portion of half a radular transverse row; numbers denote position of tooth from the central tooth. E, *Lymnaea stagnalis*, section of the digestive tract. F, lymnaeid reproductive system. G, copulatory organ of *Austropeplea tomentosa*. alb, albumen gland; cae, caecum; cth, central tooth; fgo, female gonopore; gzz, gizzard; int, intestine; lth, lateral tooth; mgo, male gonopore; mth, marginal tooth; ndg, nidadmental gland; oes, oesophagus; ovd, oviduct; ovt, ovotestis; pen, penis; pgl, prostate gland; ppm, praeputium; psh, penial sheath; sev, seminal vesicle; vag, vagina; vas, vas deferens. (D, G, after Hubendick 1951; E, F, after [A–C, R. Plant; D, H. B. Scott; F, G, C. Eadie] Hubendick 1978)

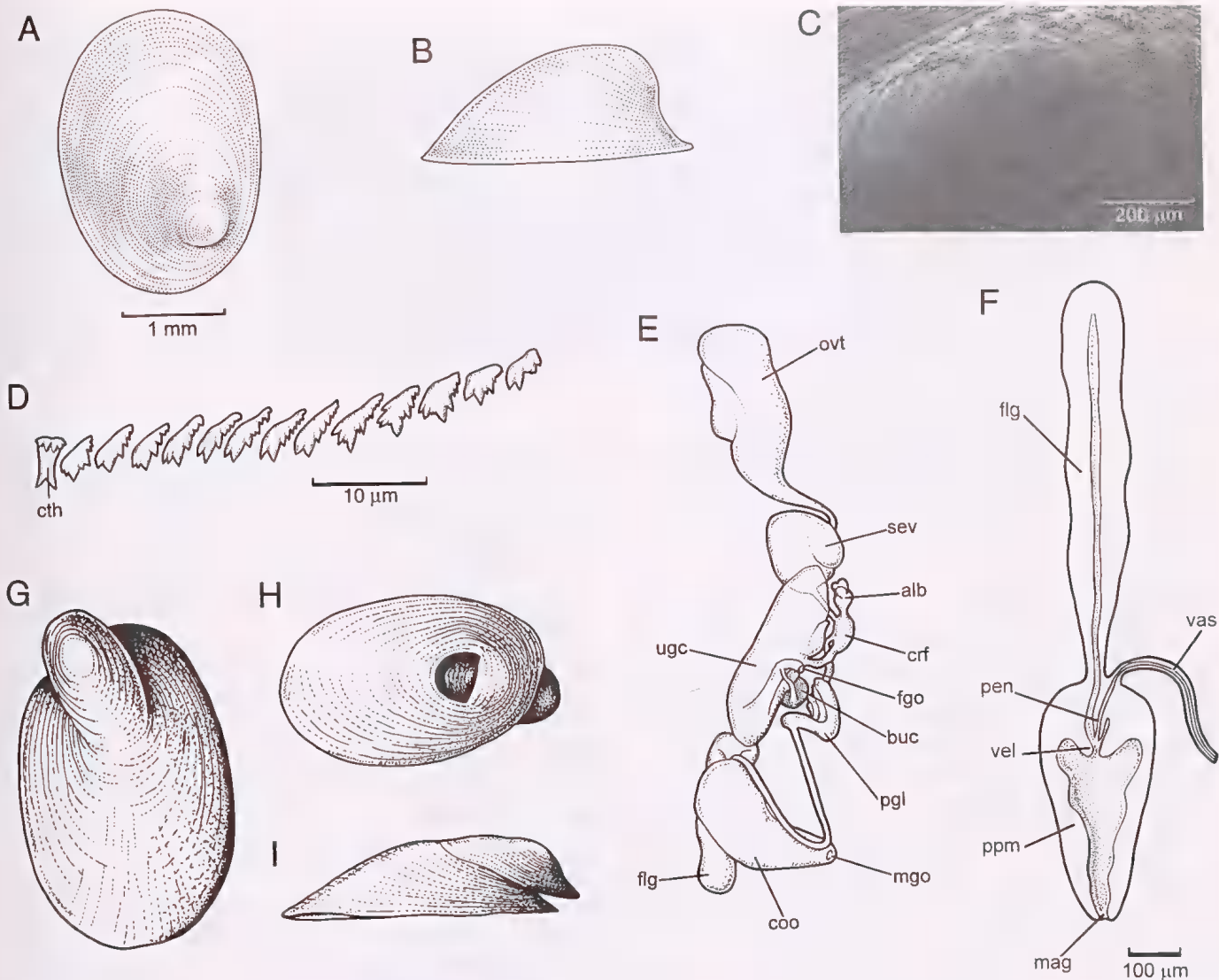


Figure 17.32 Family Ancyliidae. Freshwater limpets. A–F, *Ferrissia tasmanica*: A, shell, dorsal view; B, shell, lateral view; C, apical sculpture; D, half of a radular transverse row; E, reproductive system; F, copulatory organ. G–I, *Ferrissia petterdi*, shell, showing septation: G, dorsal view; H, ventral view; I, lateral view. alb, albumen gland; buc, bursa copulatrix; coo, copulatory organ; crf, carrefour; cth, central tooth; flg, flagellum; fgo, female gonopore; mgo, male gonopore; ovt, ovotestis; pen, penis; pgl, prostate gland; ppm, praeputium; sev, seminal vesicle; ugc, uterine gland complex; vas, vas deferens; vel, velum. (D–F, after Hubendick 1960; G–I, after Hubendick 1967)

Lymnaeids are strictly freshwater and live in a variety of lotic and lentic habitats ranging from flowing streams to warm stagnant ponds and thrive in eutrophic conditions (Smith & Kershaw 1979). The shells are ecophenotypically variable and self-fertilisation has led to many localised populations with distinctive shell morphology.

Species of this family are important vectors of parasites. *Austropeplea tomentosa* and *Pseudosuccinea columella* are intermediate hosts in the life cycle of the liver fluke *Fasciola hepatica* in sheep and cattle (see also Chapter 1; Boray & McMichael 1961; Ponder 1975). Hence the family has major economic importance in Australia.

The distribution of this family is almost worldwide. Two subfamilies are recognised – the cosmopolitan Lymnaeinae and the patelliform, North American, Lanciae. In Australia, lymnaeids are widespread along the eastern half of the continent. The introduced *P. columella* has also been recorded from the south-western region (Chalmer & Kendrick 1975). *Austropeplea tomentosa* is mainly found in south-eastern Australia but is also native to New Zealand (Boray & McMichael 1961). *Austropeplea lessoni* is more widespread and has been recorded also from New Guinea (Bentham Jutting 1963). Zilch (1959) associated *Austropeplea* with the Euro-Asian genus *Myxas*. However, Burch & Patterson (1971a) indicated that the Australian species may be

related to the Asian lymnaeids grouped in *Radix*. On the basis of immunological studies, Burch & Lindsay (1973) concluded that *Austropeplea* species form a distinct group, thus reaffirming the opinion of Inaba (1969).

Family Ancyliidae

The Ancyliidae are a family of freshwater limpets characterised by small, patelliform shells that lack coiling and have an acentric, posteriorly pointing apex (Fig. 17.32A–C). An unusual aspect of the ancyloid shell is the occasional formation of a septum as a horizontal outgrowth from the posterior shell margin which closes the posterior half of the shell aperture. The animals are sinistral with the gonopores situated on the left side of the body.

Iredale (1943a) introduced two new genera and several new species in the Ancyliidae to accommodate a variety of shell forms from different geographical regions. Hubendick (1960) published an anatomical account of an Australian ancyloid from South Australia and concluded that it was only subgenerically distinct from the widespread genus, *Ferrissia*. Hubendick (1967) reviewed the Australian species and concluded that only two form-groups could be recognised – *Ferrissia petterdi* and *F. tasmanica*. McMichael (1967) presented a general review of the nomenclatural problems surrounding the Australia species; these are still unresolved. Smith (1992) listed three species in two genera.

17. PULMONATA

Septation (Fig. 17.32G–I) has led to the naming of unusual shell morphotypes. However, it has been shown that septation is affected by changing ecological factors such as oxygen content and temperature of the water (Richardot 1977a, 1977b) and its extent varies from species to species. Septation occurs occasionally in *F. petterdi*, but has not been recorded for *F. tasmanica*. As the septa form, continued growth at the margin of the reduced aperture results in a shell with a cap-like structure. This cap is the original shell. Shell sculpture consists of fine radial lines on the apex (Fig. 17.32C) and concentric growth lines lower down. Shells vary from pale yellowish-brown to colourless but are often rendered dark-brown or black by deposits.

The ancyloid head is reduced and the foot is enlarged and sucker-like. According to Hubendick (1978) the animal of *F. petterdi* is unpigmented except for the eyes; in *F. tasmanica* a black ring of pigment is present on the dorsal surface inside the mantle collar. Ancylicids have a pair of short tentacles, and the mantle cavity is greatly reduced and situated on the left side of the body where a pseudobranch (accessory gill) is present. The kidney is long and narrow and the elongate urethra opens through a tiny renal pore on the inside of the mantle collar in the left posterior third of the body (Hubendick 1978).

The ancyloid radula consists of central teeth with two prominent cusps and several smaller denticles (Fig. 17.32D) and multicuspidate lateral and marginal teeth. The horseshoe-shaped jaw is lined with numerous minute plates (Bentham Jutting 1956). Ancylicids have a thin-walled crop, a cylindrical gizzard and the intestinal region of the stomach receives a single duct from the digestive gland. A well-developed gastric caecum is present.

Ancylicids are hermaphroditic with a partly diaulic reproductive system (Fig. 17.32E) and may or may not (aphally) have a penis. If a penis is present then a flagellum is also present (Fig. 17.32F). In *Ferrissia* species, a male copulatory organ is present (Hubendick 1978). Eggs are laid in gelatinous capsules which may contain a single egg or several eggs (Bentham Jutting 1956). These are deposited on water plants, stones or timber.

Ancylicids inhabit lotic and lentic freshwaters which vary from stagnant pools to flowing creeks and rivers, and are usually found attached to rocks, wood or vegetation.

The family has a worldwide distribution. Iredale (1943a) isolated the Australian species as a separate biogeographical unit. By placing the species in *Ferrissidae*, Zilch (1959) suggested quite diverse relationships for the Australian fauna. However, Hubendick (1967) has indicated that the Australian species are related to an ancyloid fauna present in the Pacific and Neotropical regions of the world.

As interpreted by Hubendick (1967), *Ferrissia petterdi* occurs over most of Australia and may be conspecific with the New Zealand *Ferrissia neozelanica*; and *Ferrissia tasmanica* is known from the eastern half of the Australian continent and from Papua New Guinea (Hubendick 1967). However, this interpretation has yet to be tested using modern techniques.

Hubendick (1978) suggested that this family should be united with the Planorbidae. However, this view has not been readily adopted by other workers and the traditional view of Zilch (1959) is maintained.

Family Planorbidae

Planorbid pulmonates are freshwater forms with sinistral, flat, discoidal, patelliform, ovate or turreted shells (Figs 17.33A–H, 17.34). Dextral shells occur in some groups, but, like ancylicids, the animal is always sinistral with the pulmonary cavity and major openings on the left side.

Iredale (1943a) confusingly listed numerous species under several family categories (Bullinidae, Planorbidae, Ancylicidae). Many of the generic groupings used by Iredale (1943a, 1943b, 1944b) implied that the Australian planorbid fauna forms a distinct

geographical unit. F.C. Baker (1945) partially monographed the family but included only limited references to Australian species. McMichael (1967) presented a critical appraisal of the nomenclatural problems associated with the Australian species and indicated possible extralimital relationships.

The Australian representatives of this family exhibit three basic shell forms (Fig. 17.33A–H). These are patelliform (*Ancylastrum*), planate (*Helicorbis*, *Gyraulus*) and elongate-conical (*Isidorella* and others). Smith & Kershaw (1979) provided a useful guide to the various forms. Shell sculpture is variable and may consist of obvious ridges and fine growth lines (*Glyptophysa*, *Ancylastrum*) or transverse ridges (*Gyraulus*). The shell may be glossy and smooth (*Helicorbis*) or may have periostracal hairs (*Isidorella* and *Glyptophysa*). Peripheral keels are present in *Gyraulus* and *Helicorbis*. In elongate-conical forms, the spire may be short (*Amerianna*) or attenuate.

Brown (1981) revised several Australian planate planorbids and concluded that probably only two genera – *Gyraulus* and *Helicorbis* – are valid. Walker (1984) grouped the Australian non-planate planorbids into a number of genera on the basis of anatomy. Walker's (1988) classification, based on his comprehensive generic review of these groups, is used here. Smith (1992) listed 10 genera and 41 species, including the introduced *Planorbarius corneus*.

The foot of the animal is small and broad, and the tentacles are long and slender. Most species have a pseudobranch below the pulmonary orifice on the left side (Fig. 17.33I–K). The mantle cavity is a narrow tube in discoidal planorbids, and in the high-spired forms is a triangular cavity. The roof of the mantle cavity is pigmented in some species. The kidney is elongate, and looped in discoidal forms. It is often divided into a proximal sac-like region and a distal tubular portion which is reflected as a urethra. The renal pore is located on the inside of the mantle collar.

The radula consists of straight transverse rows of teeth. The central teeth are usually bicuspidate, the lateral teeth tricuspidate and the marginal teeth serrate (Fig. 17.33L–N). The jaw consists of a central transverse piece, slightly arched, and two lateral appendages (Fig. 17.33O). Between the oesophagus and the gizzard there is a thin-walled crop. The gizzard consists of two well-developed muscle pads; a caecum is present. The digestive gland is unilobed and has only a single opening to the stomach (Hubendick 1978).

Planorbids are hermaphroditic with a diaulic reproductive system below the albumen gland. The copulatory organ of *Glyptophysa* is characterised by the presence of a large flagellum (Fig. 17.33S). Apart from relatively minor differences, *Ancylastrum* and *Opplatoria* have a similar male reproductive organ (Fig. 17.33Q). *Bayardella* has a copulatory organ with an accessory bursa (Fig. 17.33R), *Isidorella* has a normal pendant penis (Fig. 17.34), and *Amerianna* has a true penis with the opening of the vas deferens terminal (Fig. 17.33P). The penis of *Gyraulus* has a terminal stylet (Fig. 17.33T–V). *Helicorbis* does not have a penial stylet but the penis sheath bears two adpressed flagella. The male gonopore is just posterior of the left tentacle and the female gonopore is on the neck near the base of the pseudobranch. Eggs are laid in gelatinous masses.

Planorbids have a worldwide distribution. In Australia they are the dominant group of freshwater molluscs in many areas. They are confined to waters of low salinity and are usually associated with macrophytes or algae on which they browse (Smith & Kershaw 1979).

Certain planorbid snails, such as the African *Biomphalaria glabrata* and *Bulimus* species, are vectors of the blood fluke *Schistosoma* (bilharzia) in humans. Although this disease is not established in Australia, the possibility that Australian species can act as vectors for *Schistosoma mansoni* has yet to be discounted. For further information on the economic significance of planorbids see Chapter 1.

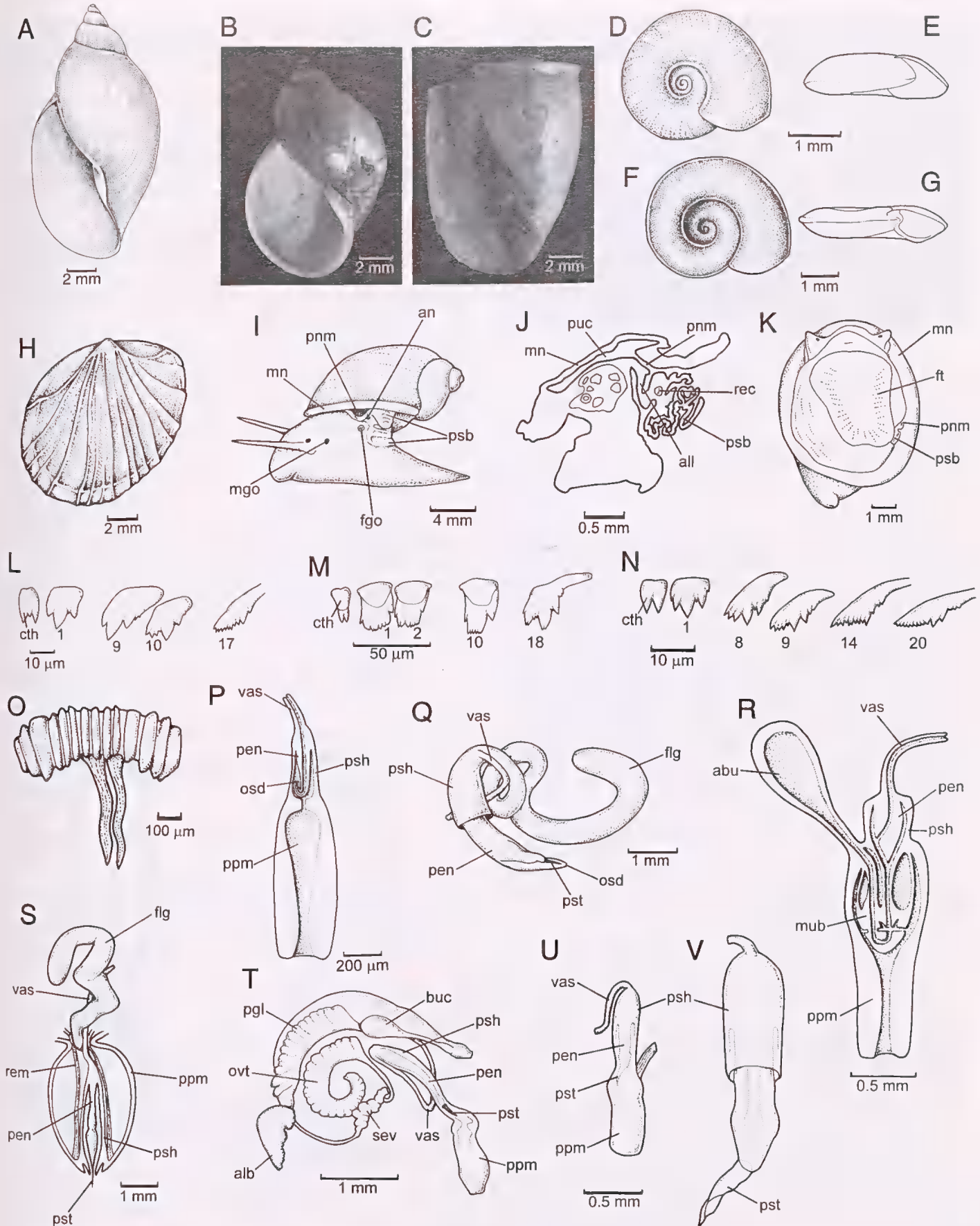


Figure 17.33 Family Planorbidae. A–H, shells showing the three categories of shell shapes found in the family. A–C, elongate-conical shells, apertural views: A, *Glyptophysa concinna*; B, *Isidorella newcombi*; C, *Amerianna carinata*. D–G, planate shells: D, E, *Helicorbis australiensis*, apical (D) and apertural (E) views; F, G, *Gyraulus meridionalis*, apical (F) and apertural (G) views. H, patelliform shell, *Ancylastrum irvinae*, dorsal view. I, *Isidorella newcombi*, lateral view showing pseudobranch and location of gonopores. J, *Isidorella newcombi*, transverse section through the pulmonary cavity. K, *Ancylastrum irvinae*, ventral view, showing the position of the pneumostome. L–N, portions of half radular transverse rows, numbers denote position of tooth from the central tooth: L, *Isidorella newcombi*; M, *Ancylastrum irvinae*; N, *Amerianna carinata*. O, *Ancylastrum irvinae*, jaw. P–S, copulatory organs: P, *Amerianna carinata*; Q, *Ancylastrum irvinae*; R, *Bayardella johni*; S, *Glyptophysa aliciae*. T, reproductive tract; *Gyraulus waterhousei*. U, V, *Gyraulus isingi*: U, penis shown in position inside the penis sheath; V, penis everted. abu, accessory bursa; alb, albumen gland; all, anal lobe; an, anus; buc, bursa copulatrix; cth, central tooth; fgo, female gonopore; flg, flagellum; ft, foot; mgo, male gonopore; mn, mantle; mub, muscular bulb; osd, opening of vas deferens; ovt, ovotestis; pen, penis; pgl, prostate gland; pnm, pneumostome; ppm, praeputium; psb, pseudobranch; psh, penis sheath; pst, penial stylet; puc, pulmonary cavity; rec, rectum; rem, retractor muscle; sev, seminal vesicle; vas, vas deferens. (D–G, after Smith & Kershaw 1979; H–N, P–S, after Walker 1988; O, after Hubendick 1978; T–V, after Brown 1981) [A, R. Plant; B, C, Queensland Museum; D–V, B. Scott]



Figure 17.34 Family Planorbidae. *Isidorella newcombi* lives in lentic freshwater in southern and eastern areas of Australia including the Murray-Darling River system. Here it is shown with its copulatory organ everted. [J. Walker]

The use of the African genus *Bulinus* for non-planate Australian planorbids implied a relationship between these two faunal groups (Hubendick 1948, 1955). McMichael (1967) considered that the Australian planorbids are more closely related to widespread Asian and Pacific groups and that they arrived from the north in the late Tertiary. With the possible exception of *Pygmanisus*, the Australian planate planorbids are probably related to groups widespread outside Australia rather than to African endemic groups (Brown 1981). Walker (1984) discussed the biogeography of the Australian buliniform planorbids and concluded that they had quite diverse origins. *Isidorella*, *Bayardella* and *Glyptophysa* (= *Physastra*) are probably Gondwanan relicts. *Glyptophysa* has subsequently radiated into the Pacific Basin and Indonesian island arc. *Oppletora* and the geographically restricted *Ancylastrum* – recorded only from highland streams and lakes in Tasmania – are local derivatives of *Glyptophysa* stock whereas *Amerianna* probably arose in the New Guinea–northern Australian region. In addition to these endemic groups, several introduced species are also now included in the Australian fauna.

The fossil record of the Planorbidae in Australia includes *Physastra rodingae* from the Tertiary of northern Australia. Several other fossil planorbids (*Gyraulus chapmani*, *Syrioplanorbis hardmani*, *Isidorella* sp.) were present with *P. rodingae* (see McMichael 1968), but their relationships to extant species are uncertain.

Family Physidae

Physids are freshwater snails that have thin, sinistral, elongate-conical, imperforate shells (Fig. 17.35A). The spire is usually elevated and sculpture is lacking. A columellar callus may be present and the aperture is large.

This family of snails is not native to Australia. Early literature records of species assigned to the European genus *Physa* belong to Planorbidae. However, true physids have been introduced to Australia (Smith & Kershaw 1979) and their shells are easily confused with planorbid species belonging to *Glyptophysa* and *Isidorella*. Nevertheless, there are many anatomical features which differentiate the two families (see below). These were discussed by Smith & Kershaw (1979) who recognised a single introduced species, *Physa acuta*, in south-eastern Australia. Some authors, for example, Burch & Tottenham (1980), placed this species in *Physella*. This allocation is followed in preference to that of Smith (1992).

The shell of *Physella acuta* is small (12–15 mm in height) smooth and almost transparent, and thus the mottled colouring of the mantle is readily visible through the shell. The tentacles are long and filiform. The mantle margin has several digitations (Fig. 17.35B) unlike that of planorbids which is straight. There is

no pseudobranch. The kidney forms a strongly convoluted duct on the internal surface of the mantle. The blood is clear. The ureteric pore is situated near the pneumostome.

The physid radula is divided and divergent posteriorly with tooth rows arranged obliquely. The central teeth are denticulate and the lateral teeth are multicuspidate. These features distinguish the physids from planorbids which have a horizontally arranged, non-divided radula. The lateral and marginal teeth have unusual basal appendages. The jaw is solid, very small and consists of numerous plates.

The stomach consists of three parts with a thin-walled crop between the oesophagus and a weakly developed gizzard. The digestive gland is bilobed and opens into the stomach through two ducts.

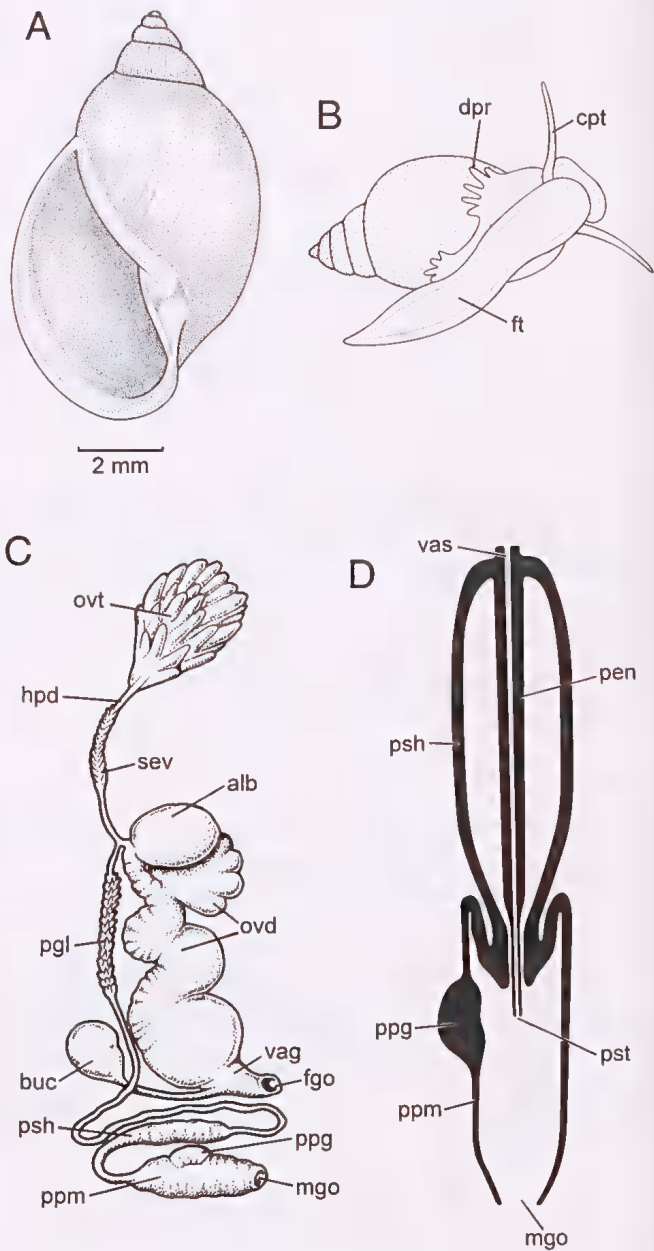


Figure 17.35 Family Physidae. A, *Physella acuta*, shell, apertural view. B, *Physa* sp., ventral view, showing digitate mantle processes. C, D, *Physa fontinalis*, a European species, reproductive anatomy: C, reproductive tract; D, copulatory organ. alb, albumen gland; buc, bursa copulatrix; cpt, cephalic tentacle; dpr, digital processes on mantle; fgo, female gonopore; ft, foot; hpd, hermaphroditic duct; mgo, male gonopore; ovd, oviduct; ovt, ovotestis; pen, penis; pgl, prostate gland; ppg, praeputial gland; ppm, praeputium; psh, penis sheath; pst, penial stylet; sev, seminal vesicle; vag, vagina; vas, vas deferens. (A, after Burch & Tottenham 1980; B, after Hyman 1967; C, D, after Duncan 1958) [A, B, D, C. Eadie; C, B. Scott]

Physids exhibit an intermediate stage between simultaneous and protandric hermaphroditism (Hubendick 1978). Both cross-fertilisation and self-fertilisation are common, with the latter dominant in some species (Duncan 1958). The reproductive system is diaulic (Fig. 17.35C). The prostate gland is a series of invaginations of the vas deferens. The penis has a well-developed sheath and praeputial gland (Fig. 17.35D). The gonopores are situated on the left side – the male below the tentacle base and the female at the edges of the mantle collar. The eggs are transparent and are laid in a gelatinous mass.

Physella acuta lives on weeds and other substrata in freshwater ponds and fast and slow-flowing streams. They are also present in disturbed habitats.

The family has a basically Holarctic and Neotropical distribution. Smith & Kershaw (1979) suggested that the Australian introduction came from Western Europe. *Physella acuta* is established in south-eastern Australia, particularly in areas associated with human activity; it is now one of the most common freshwater snails in the Sydney area. Although there are no literature records regarding its distribution elsewhere in Australia, specimens have been collected from south-eastern Queensland and it is highly probable that *P. acuta* also occurs in other densely populated centres.

Superfamily GLACIDORBOIDEA

Glacidorboideans are very small, freshwater pulmonates that have a dextrally coiled shell with an operculum. The head has a pair of non-invaginable, strongly ciliated, cephalic tentacles which have eyes at their bases. The pallial cavity is open and lacks a pneumostome. There is no ctenidium. The radula consists of many rows of a triangular central tooth, with or without lateral teeth. Glacidorboideans are hermaphrodites with separate male and female reproductive tracts and separate gonopores.

Earlier authors considered *Glacidorbis* to be a highly modified prosobranch (Haszprunar 1988). The placement accepted here, however, follows that of Ponder (1986). A single family with members distributed in southern Australia and South America is included.

Family Glacidorbidae

Glacidorbids are freshwater snails which have a planispiral shell and an operculum. The shell is very small, and is generally smooth, but with prominent growth lines. The coiling is dextral with 2.5 to 3 whorls. The protoconch is granular to smooth and not greatly differentiated from the teleoconch. The operculum is thin, corneous and paucispiral (Fig. 17.36D).

Glacidorbis was erected by Iredale (1943a) as a genus in the Planorbidae for the species *G. hedleyi*. Smith (1973, 1979a) added two more species from Tasmania. Smith (1973) described the radula and operculum of the Tasmanian species, *G. pedderi*, and Meier-Brook & Smith (1975) described the radula and operculum of *G. magellanicus* from South America. These authors tentatively assigned *Glacidorbis* to the Hydrobiidae. This view was supported by Smith (1979a). Bunn & Stoddardt (1983) described an additional species from south-western Australia. Ponder (1986) presented a detailed review of the anatomy of *G. hedleyi* and consequently assigned *Glacidorbis* to a new family, the Glacidorbidae, which he placed among the Basommatophora. Haszprunar (1988), based mainly on the nature of the central nervous system, placed the family in the Allogastropoda between the Rissoellidae and Pyramidelloidea, but the system of Ponder (1986) is followed here.

Glacidorbid shells are dextral, simple planispiral and are either keeled (*G. pedderi*) or rounded (Fig. 17.36A–C). The eyes are situated in the middle of the cephalic tentacle bases. The tentacles are not capable of invagination and are strongly ciliated. The animal's snout and anterior sides of the foot are usually pale to dark grey. The mantle roof is pigmented black and grey, and is

visible through the shell. The foot is broad with an indented anterior margin and two lateral processes. The sole lacks pedal glands posteriorly. The pallial cavity is open and large. There is no pneumostome. The kidney, which is visible through the shell, lies in the right side of the pallial roof (Fig. 17.36G). There is no ctenidium, osphradium or hypobranchial gland. Water movement in the pallial cavity is due to currents created by cilia on a mantle lobe (Ponder 1986).

The radula consists of more than 20 rows of single central teeth each of which has a large triangular, recurved mesocone and a row of denticles along each postero-lateral margin (Fig. 17.36E, F). No marginal or lateral teeth are present in the Australian species, but the radular membrane on each side of the central tooth may consist of untanned plates. There are no odontophoral cartilages. The jaw consists of paired dorsal and ventral elements. The buccal mass is short, the stomach is small and the digestive gland is simple and tubular. There is neither a gizzard nor a crop. The anus opens about halfway along the pallial cavity (Fig. 17.36G).

The glacidorbid nervous system has only four ganglia in the visceral loop and displays a remnant of chiasmoneury. The small osphradial ganglion is situated at the left side. There is no trace of a procerebrum or a cerebral gland or of so-called dorsal bodies (Haszprunar 1988).

Glacidorbids appear to be protandrous hermaphrodites (Fig. 17.36H; Ponder 1986). The gonad is sac-like and situated above the digestive gland. In mature females, a large semi-translucent albumen gland and multilobed capsule gland open into a thin-walled vestibule prior to joining a short, wide vagina (Fig. 17.36I). The female gonopore is situated at the posterior end of the pallial lobe. In mature males, the prostate gland is elongate, lying half in the floor of the pallial cavity and half in the visceral mass. The hermaphroditic duct enters halfway down its length and a narrow tubular vas deferens emerges near the point of entry of that duct. The penis has an apical muscular bulb with attached retractor muscle and anterior thin-walled sheath. Internally the penis has numerous sucker-like penial glands (Fig. 17.36J). The male gonopore is situated just below the right tentacle. A well-developed seminal vesicle is present in mature males. The hermaphroditic duct is thick-walled in its lower sections and even thicker walled near its junction with the gonad. This may be the site of fertilisation (Ponder 1986).

In *G. hedleyi*, the encapsulated eggs are brooded within the pallial cavity and display various stages of development from embryo to shelled juvenile (Ponder 1986). Viviparity has been noted in other species of *Glacidorbis* and Smith (1979a) reported finding developing embryos in the uterus of *G. paupela*.

Species of *Glacidorbis* live in a variety of freshwater habitats including swamps, lakes and streams, and are usually associated with decaying vegetable material (Smith 1979a; Bunn & Stoddard 1983). Smith (1985) suggested that *G. hedleyi* and *G. occidentalis* may be able to withstand desiccation in intermittent stream habitats.

Ponder (1986) considered that the diet of glacidorbids includes a variety of wounded invertebrates including pisidiid bivalves, other *Glacidorbis*, beetle larvae and amphipods. In the laboratory, however, *Glacidorbis* showed no liking for plant material or dead, decaying animals.

The occurrence of the species in south-eastern and south-western Australia and South America suggests a relict Gondwanan distribution. The South American *G. magellanicus* has not been dissected and a more comprehensive analysis of relationships will not be possible until this species has been studied in detail. A single fossil species has been recorded from northern South Australia (Buonanito, in Bunn & Stoddard 1983).

17. PULMONATA

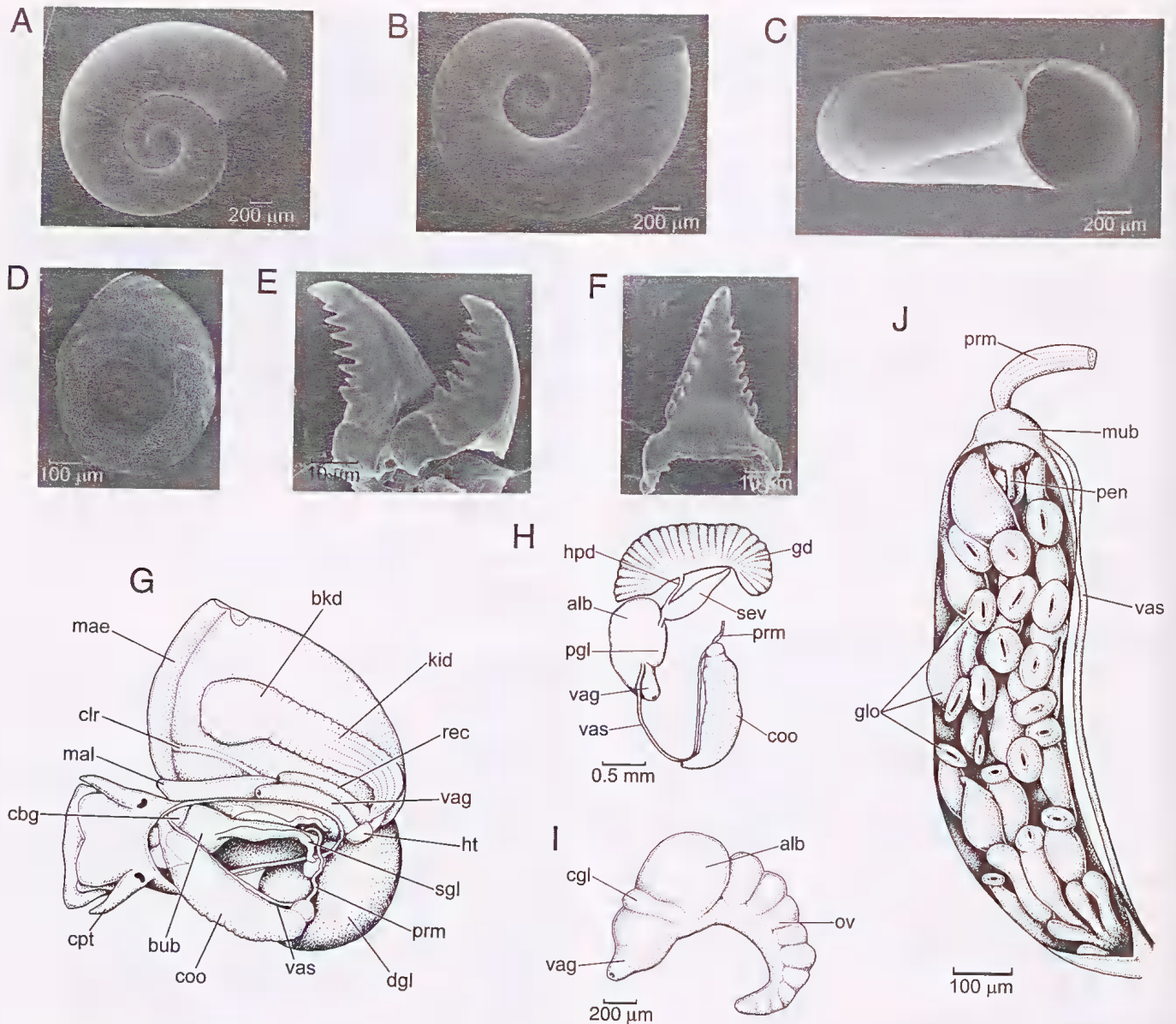


Figure 17.36 Family Glacidorbidae. *Glacidorbis hedleyi*: A, shell, apical view; B, shell, umbilical view; C, shell, apertural view; D, operculum; E, radular teeth, lateral view; F, radular tooth, ventral view; G, mantle cavity; H, reproductive tract of a male during the transition to a female system; I, reproductive tract of a mature female; J, details of copulatory organ. alb, albumen gland; bkd, bladder like region of kidney; bub, buccal bulb; cbg, cerebral ganglia; cgl, capsule gland; clr, ciliated ridge; coo, copulatory organ; cpt, cephalic tentacle; dgl, digestive gland; gd, gonad; glo, glands of copulatory organ; hpd, hermaphroditic duct; ht, heart; kid, kidney; mae, mantle edge; mal, mantle lobe; mub, muscular bulb of the penis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; rec, rectum; sev, seminal vesicle; sgl, salivary gland; vag, vagina; vas, vas deferens. (A–F, from Ponder 1986; G–I, after Ponder 1986) [G–J, B. Scott]

Order EUPULMONATA

Eupulmonates usually have a spirally coiled shell, although this is modified or absent in some groups. The eyes are located either at the base of contractile tentacles or on the tips of a pair of invaginable tentacles. The shell is commonly dextral. An operculum is nearly always absent in adults. A contractile pneumostome is present and there is no osphradium and no ciliary tracts in the pallial cavity. The central nervous system is hypoathroid (adjacent pleural and pedal ganglia) and the procerebrum contains both large nerve cells and globineurons (Haszprunar & Huber 1990).

Nordsieck (1992) combined the Eupulmonata (*sensu* Haszprunar & Huber) and the Systellommatophora (+ Otinidae) into a superorder of equal rank to the Basommatophora. However, the more conservative approach of Haszprunar & Huber (1990) is followed here. The three suborders within the Eupulmonata are the Actophila, Trimusculiformes and Stylommatophora.

Eupulmonates live in marine or terrestrial, including arboreal, habitats. The earliest fossil record is of a species in the Stylommatophora from the late Palaeozoic of the Northern Hemisphere.

Suborder ACTOPHILA

Superfamily ELLOBIOIDEA

Ellobioideans are marine or rarely terrestrial pulmonates with spirally coiled shells which are usually dextral. The aperture usually has lamellae and/or tiny denticles. Each cephalic tentacle is cylindrical with an eye at the inner base. Ellobioideans are hermaphrodites with separate male and female gonopores and a primitive reproductive system (Morton 1955b). The superfamily includes one family – the Ellobiidae, which is largely intertidal and has radiated extensively in the Indo-Pacific region.

Although Hubendick (1978) treated ellobioids as basommatophorans, Haszprunar & Huber (1990) placed them in the Eupulmonata with the Stylommatophora on the basis of their central nervous system which has the pedal ganglia adjacent to the pleural ganglia (hypoathroid).

Family Ellobiidae

Ellobiids have a high-spired, dextral and comparatively thick-walled shell (Fig. 17.37A–H; Pl. 31.4). Most species have well-developed palatal, parietal and/or columellar teeth. The

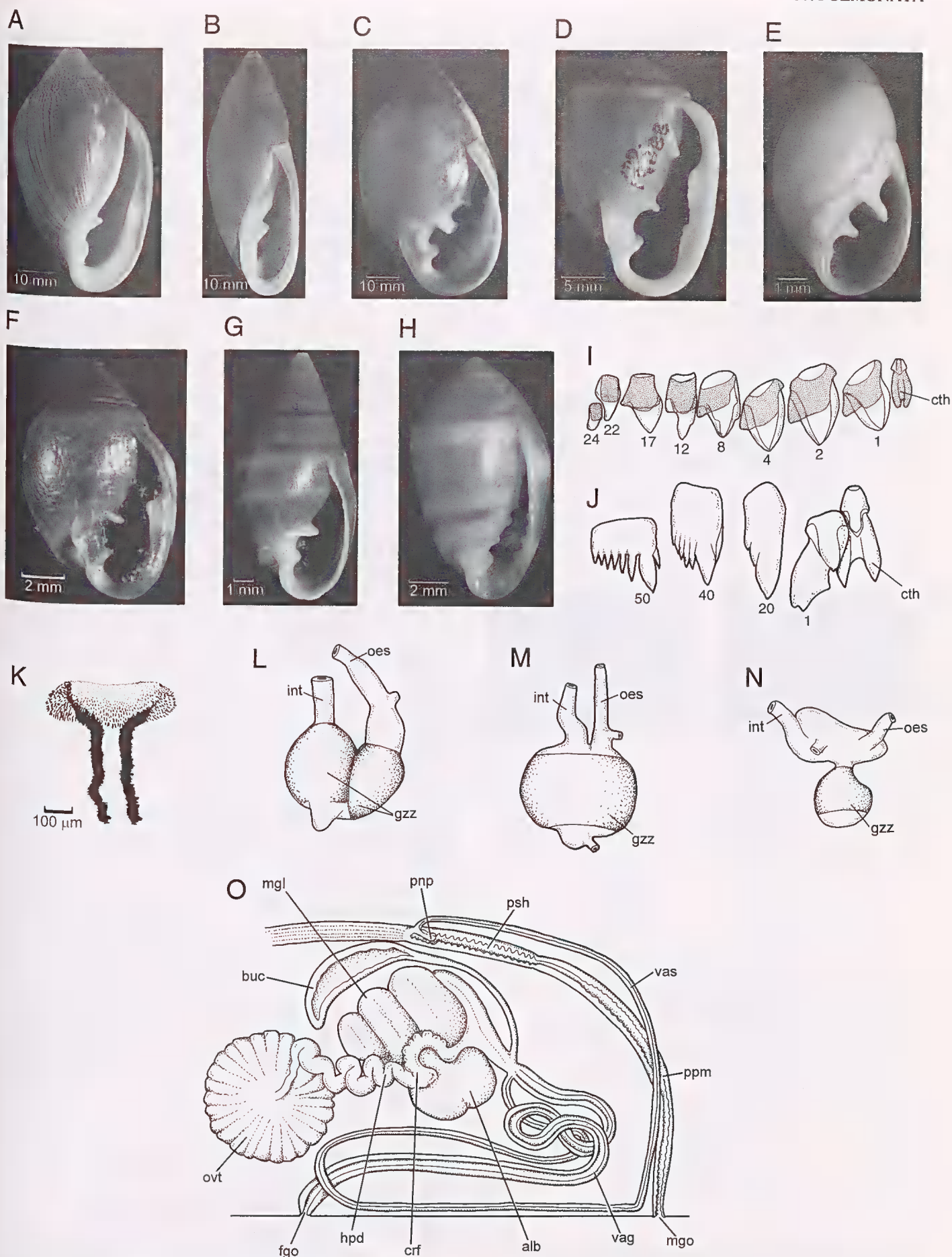


Figure 17.37 Family Ellobiidae. A–H, shells, apertural views showing the apertural folds and teeth: A, *Ellobium aurismidae*; B, *Ellobium aurisjudae*; C, *Pythia scarabaeus*; D, *Cassidula angulifera*; E, *Marinula xanthostoma*; F, *Melosidula zonata*; G, *Ophicardelus ornatus*; H, *Melampus fasciatus*. I, J, halves of one radular transverse row: I, *Ellobium pellucens*; J, *Melampus coffeus*. K, *Melampus fasciatus*, jaw. L–N, different stomach configurations: L, *Ovatella myosotis*; M, *Ellobium pellucens*; N, *Melampus* sp. O, *Melampus coffeus*, reproductive tract. alb, albumen gland; buc, bursa copulatrix; crf, carrefour; cth, central tooth; fgo, female gonopore; gzz, gizzard; hpd, hermaphroditic duct; int, intestine; mgl, mucous gland; mgo, male gonopore; oes, oesophagus; ovt, ovotestis; pnp, penial papilla; ppm, praeputium; psh, penis sheath; vag, vagina; vas, vas deferens. (I, after Marcus, Ev. & Marcus, Er. 1965b; J, O, after Marcus, Ev. & Marcus, Er. 1965a; K–N, after Hubendick 1978)

[A–H, Queensland Museum; I–O, B. Scott]

17. PULMONATA

family is further characterised by the gradual resorption of internal shell structures during growth. The shells of *Pythia* species are compressed.

Four subfamilies are recognised – the Melampinae, Pedipedinae, Ellobiinae, and the largely Holarctic, terrestrial Carychiinae. The first three of these are represented in Australia. Relationships within the family still need to be determined accurately by further comparative studies. Morton (1955a) presented significant phylogenetic discussion on the group. The Ellobiidae are characterised by a number of primitive features (Hubendick 1978), but include diverse morphological types, adapted to a wide range of environments.

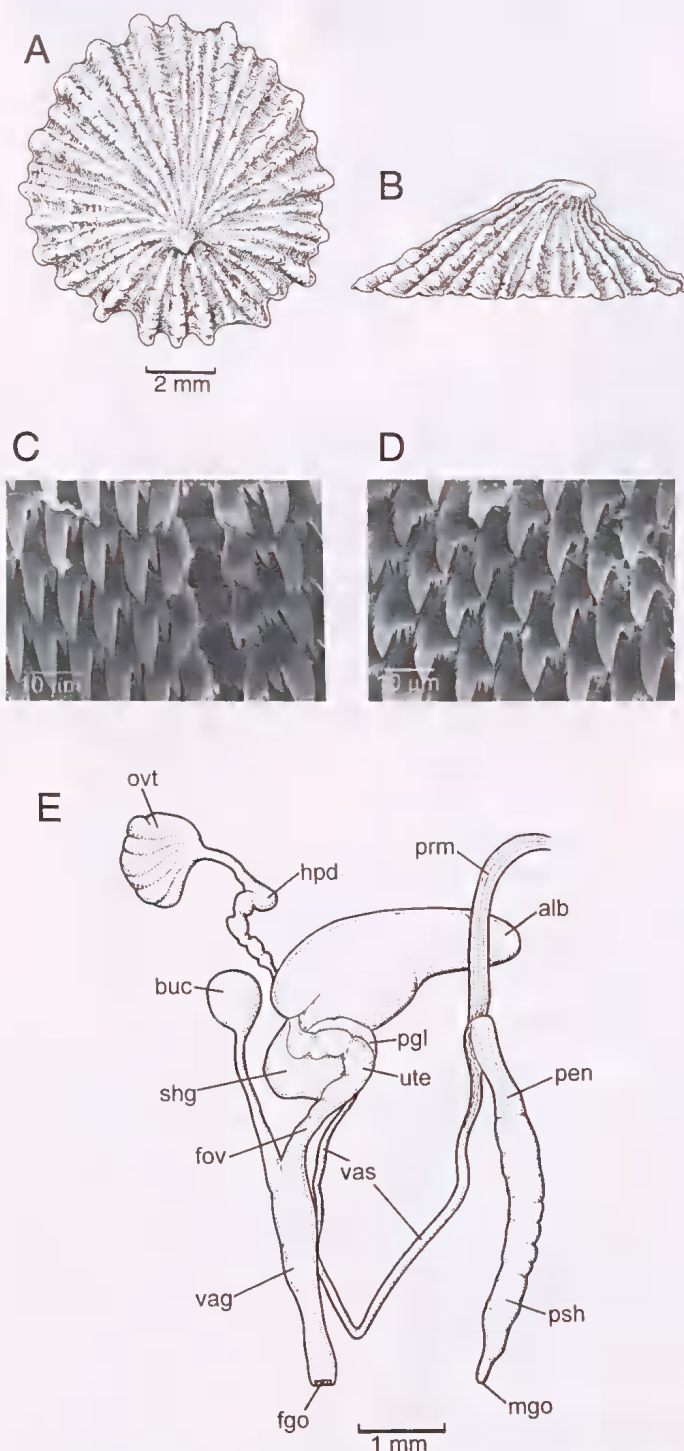


Figure 17.38 Family Trimusculidae. *Trimusculus conica*, the only species found in Australia: A, shell, dorsal view; B, shell, lateral view; C, portion of radula showing central and lateral teeth; D, portion of radula showing marginal teeth; E, reproductive system. alb, albumen gland; buc, bursa copulatrix; fgo, female gonopore; fov, free oviduct; hpd, hermaphroditic duct; mgo, male gonopore; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; psh, penis sheath; shg, shell gland; ute, uterus; vag, vagina; vas, vas deferens.

[A, B, R. Plant; C, D, Queensland Museum; E, B. Scott]

Australian species include representatives of widespread marine genera such as *Ellobium* (Fig. 17.37A, B), *Melampus* (Fig. 17.37H), *Marinula* (Fig. 17.37E), *Cassidula* (Fig. 17.37D; Pl. 31.4), *Pythia* (Fig. 17.37C) and *Laemodonta*, but their level of representation is not well known. No comprehensive review of the Australian species has been completed. Iredale (1926) revised *Ophicardelus* and Hubendick (1956) reviewed *Laemodonta* (= *Plecotrema*). No completely terrestrial species are known from Australia.

Some ellobiids, such as *Melampus* species, have distinctively coloured shells, but the majority are monochrome. Shell sculpture varies from smooth to strongly lirate. Apertural barriers are simple and few in number (for example, *Cassidula*, Fig. 17.37D and *Ophicardelus*, Fig. 17.37G), or numerous, as in *Melampus* (Fig. 17.37H). The tentacles of some ellobiids are thickened terminally and can be retracted (Marcus & Marcus 1965a). Sometimes the sole of the foot is divided ventrally into anterior and posterior sections. The mantle cavity shows no unusual features, except in species of *Melampus* which feature pneumostomal glands (Marcus & Marcus 1965a). Morton (1955b) recorded a pallial gland in *Pythia*, which may be homologous with the hypobranchial gland of the terrestrial *Carychium* (Hubendick 1978).

The ellobiid radula (Fig. 17.37I, J) varies from a primitive pulmonate type with numerous small, simple, similarly shaped teeth, to one in which the teeth are few and more differentiated. The jaw (Fig. 17.37K) consists of tiny bars which may be more or less fused. The central radular tooth is usually simple and unicuspidate; the laterals are bicuspidate with or without a split ectocone; and the marginals sometimes have numerous tiny denticles. The structure of the oesophagus and stomach vary (Fig. 17.37L–N). In *Ophicardelus*, *Cassidula* and *Pythia* the oesophageal and intestinal parts of the gizzard are distinct and muscular development is moderate. In *Ellobium* (Fig. 17.37M) and *Marinula* these sections of the gizzard have merged, and in *Melampus* the gizzard is separated from the remainder of the stomach (Fig. 17.37N; Marcus & Marcus 1965a).

Although the nervous system is typically pulmonate, that is, without crossing of the pleurovisceral connectives, the family includes taxa such as the genus *Ellobium* in which a trace of chiasmoneury is still evident. Haszprunar & Huber (1990) detailed the main characteristics of the ellobiid central nervous system.

Ellobiids are hermaphroditic and although protandry is common, examples of simultaneous hermaphroditism occur in several taxa, such as *Melampus*. A single albumen gland is usually present, but some species may have two. The genital ducts may be separate (*Ellobium*), incompletely divided (*Pythia*, *Cassidula*), or fused (*Marinula*, *Laemodonta*). In *Melampus*, the vagina is elongate and the junction between the female and spermathecal ducts is some distance from the female pore (Fig. 17.37O). The penis is muscular and has a sheath.

Australian ellobiids are mainly estuarine (for example species of *Ophicardelus*, *Cassidula*, *Ellobium*) or marine (for example, species of *Melampus*, *Laemodonta*), and less commonly, terrestrial (*Pythia* species). They live on or under stones (*Marinula* species), on the substratum (species of *Ophicardelus*, *Cassidula*), or in crevices in timber (*Melampus*). Allan (1950), Smith & Kershaw (1979), Wells (1984) and Short & Potter (1987) listed some of the more common species.

Suborder TRIMUSCULIFORMES

Superfamily TRIMUSCULOIDEA

Trimusculoidean eupulmonates have small to medium-sized, cap-like shells with prominent radial sculpture. A siphonal groove is present on the right side of the shell. The pallial cavity has no ciliary tracts or osphradium. The central nervous system is hypoathroid (Haszprunar & Huber 1990). The procerebrum has large cells and globineurons. Trimusculoideans are hermaphrodites with a partially diaulic reproductive system. A single family, the Trimusculidae, containing about 10 species, is included.

Family Trimusculidae

The family Trimusculidae is a group of marine pulmonates with cap-shaped, thick, round to ovate, small shells in which the apex is pointed posteriorly and often eroded (Fig. 17.38A, B). The sculpture is radial and a siphonal furrow is located on the right side. The shell length is usually less than 20 mm.

A single species, *Trimusculus conica*, is known from Australia. No anatomical study has been undertaken on this species. Hubendick (1946) presented a general account of the family, Schumann (1911) provided a detailed review of some South American species and Yonge (1958) recorded data on the Californian *Trimusculus reticulatus*.

Trimusculus conica is small (shell length 15 mm) and the shell surface has strong radial ribs and prominent concentric growth lines. The colour is white or cream. The interior of the shell is white and glossy, and the margins are denticulate. The siphonal groove is located much more anteriorly than in siphonariids.

The tentacles are reduced and have eyes at their bases. The mouth is anterior and ventral with a well-separated pair of oval lappets. The pulmonary cavity is large, without a gill and osphradium. The radula consists of a small central tooth and numerous denticulate lateral and marginal teeth (Fig. 17.38C, D), and there is no jaw. In *Trimusculus* the gizzard is a well-developed sac, posterior to the direct path between the oesophagus and the intestine, and posterior to the caecum. Stomach contents of *T. conica* have been shown to contain diatoms and algal spores as well as other scraped debris (Haven 1973).

Trimusculids are hermaphrodites with partially separate male and female reproductive tracts and separate gonopores (Fig. 17.38E). In *Trimusculus* the spermiduct is short and the seminal vesicle is a single branched diverticulum. The vagina is elongate and the junction between the female and spermathecal ducts is proximal to the female pore. Eggs are laid in two creamy white collars that are attached to the rocky substratum at one end and project into the pallial groove of the parent at the other. Development is direct (Haven 1973).

Trimusculids are intertidal and the Australian species occurs on exposed rocky shores of eastern and southern Australia, Lord Howe Island and Norfolk Island (Iredale 1940a). Compared with other limpet molluscs, *T. conica* is markedly immobile, and tends to occupy permanent places, glued to the substratum by a thin secretion (Haven 1973). Elsewhere trimusculids occur in the Mediterranean, on the coast of western and southern Africa, the Indo-west Pacific region, including New Zealand, and the Pacific coast of America.

Suborder STYLOMMATOPHORA

Stylommatophorans are terrestrial snails (Pls 31.2, 31.3, 32.1–32.5) with two pairs of invaginable tentacles; the eyes are situated at the tips of the superior pair. The shell is usually spirally coiled, dextral and variable in shape and size. It may be external, reduced to several internal remnants, or completely absent. An operculum is absent, although a pseudo-operculum, a modification of the posterior part of the foot, is sometimes present. Respiratory exchange takes place through a closed, vascularised pallial cavity that is modified secondarily in some groups. The stylommatophoran body plan is shown in Figure 17.39E, F.

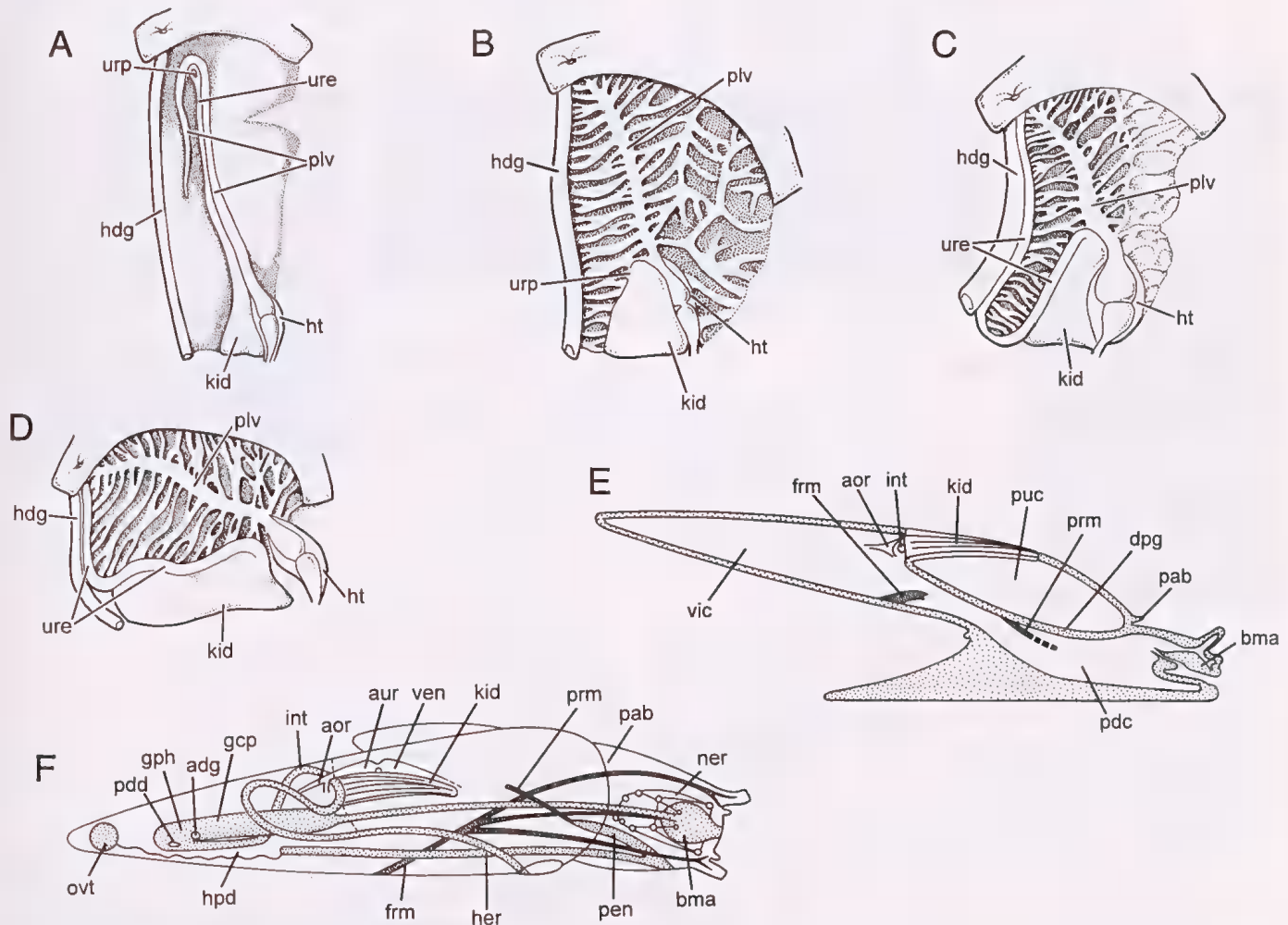


Figure 17.39 Suborder Stylommatophora. Anatomical features. A, orthurethran pallial complex. B–D, variations of the sigmorethran pallial complex: B, incomplete ureter; C, complete second ureter; D, mesurethran condition. E, F, generalised body plan: E, lateral view; F, dorsal view. *adg*, opening of anterior duct of digestive gland; *aor*, aorta; *aur*, auricle; *bma*, buccal mass; *dpg*, diaphragm; *frm*, free retractor muscles; *gcp*, gastric crop; *gph*, gastric pouch; *hdg*, hindgut; *her*, hermaphroditic portion of genital apparatus; *hpd*, hermaphroditic duct; *ht*, heart; *int*, intestine; *kid*, kidney; *ner*, nervous system; *ovt*, ovotestis; *pab*, pallial border; *pdc*, pedal cavity; *pdd*, opening of posterior duct of digestive gland; *pen*, penis; *plv*, pulmonary vein; *prm*, penial retractor muscle; *puc*, pulmonary cavity; *ure*, ureter; *urp*, ureteric pore; *ven*, ventricle; *vic*, visceral cavity. (A–D, after Solem 1959; E, F, after Tillier 1989)

The kidney is situated posteriorly on the roof of the pallial cavity. The ureter is variously configured (Fig. 17.39A–D). Stylommatophorans are hermaphrodites with a single gonopore, usually situated below the right superior tentacle. The anal and ureteric pores are typically located near the pneumostome.

Stylommatophorans are cosmopolitan and can be divided into the Orthurethra and Sigmurethra, based on patterns of excretion and water conservation (Pilsbry 1900a). A third subgrouping, the Mesurethra, has been used by some authors (Pilsbry 1900a; Zilch 1959). Mesurethrans are characterised by a triangular-shaped kidney which has a lateral opening or a short lateral protuberance. Delhaye & Bouillon (1972b) considered that mesurethrans gave rise to mainstream sigmurethrans. Solem (1959a), Smith (1992) and Nordsieck (1992) included the mesurethran families in the Sigmurethra and this classification is followed here. The Sigmurethra forms the major land snail element in most parts of the world. On some of the Pacific Islands, the Orthurethra became the dominant group. The Orthurethra is considered to be the more primitive order (Pilsbry 1900a) and the Sigmurethra the more specialised (Solem 1978a), but it is unlikely that the Orthurethra is ancestral to the Sigmurethra since there is evidence to suggest that the ultrastructure of the orthurethran kidney is different from that of the Sigmurethra (Delhaye & Bouillon 1972b). Tillier (1989) proposed a classification of the Stylommatophora, based on the structure of the pallial complex, digestive tract and central nervous system, in which he recognised the Orthurethra but replaced the Sigmurethra with the Dolichonephra and the Brachynephra. The system adopted here recognises two infraorders, the Orthurethra and Sigmurethra, within the Stylommatophora.

The Sigmurethra is the dominant stylommatophoran group in Australia with more than 800 ground-dwelling and arboreal species. There are less than 100 orthurethran species (Burch 1976b; Solem 1988b; Smith 1992). The vast majority of species are terrestrial; the group has radiated extensively in both moist and dry habitats. Several are arboreal, mainly from the wetter forests of the east coast and the northern monsoonal forests.

Relationships of the Australian families have been discussed by McMichael & Iredale (1959), Solem (1959a) and Bishop (1981). Their origins are diverse and they consist of Gondwanan relicts as well as more recent, northern invasive elements. A number of species have also been introduced by commerce and other human activity since the early 1800s. Thirty-one families are represented.

Infraorder ORTHURETHRA

The Orthurethra is a group of very small to medium-sized snails, with spirally coiled shells which are variable in shape, and either sinistral or dextral. The aperture may be narrowed by the presence of lamellae and denticles. The kidney tapers anteriorly into the ureter which typically leads directly forward, remote from the hindgut, and opens within the forward border of the lung (Pilsbry 1948). In some enids (Solem 1964b) a pseudosigmurethrous ureter is developed. The foot is holopodous.

Solem (1978a) considered that the presence of the pseudosigmurethrous condition indicates that the Orthurethra was a separate evolutionary experiment in water retention from the event that resulted in the typical Sigmurethra. Within the Orthurethra, relationships between the various groups are still problematic. It is possible that the anatomical similarities are convergent and not representative of a single major conservative trend in water resorption. Until some of the groups are examined in more detail, these basic uncertainties will remain.

The Orthurethra includes some arboreal species, but does not include any species with reduced shells, such as slugs or semi-slugs.

Orthurethran snails have been recorded from Upper Carboniferous coal beds of Europe and North America (Solem & Yochelson 1979). Today the Orthurethra is distributed worldwide and is represented by four superfamilies, all of which occur in Australia.

Superfamily ACHATINELLOIDEA

Achatinelloids are small to medium-sized snails with dextral or sinistral shells that may or may not be brightly coloured. In most taxa, the aperture contains variously positioned lamellae. The lip is either simple or thickened and reflected. The radula consists of many rows of rastriform teeth. The ureter has a narrow recurved ridge at the tip. A penis is usually present and often lacks an epiphallus. A penial appendix may or may not be present. Achatinelloideans are hermaphroditic and may be oviparous or viviparous.

A single family, the Achatinellidae, is included (Cooke & Kondo 1960). This is probably a primitive group of great antiquity.

Family Achatinellidae

Achatinellids are arboreal and ground-dwelling terrestrial land snails with very small to medium-sized shells that are ovate-conic to turreted in form. Many extralimital species have brightly coloured shells, but those of Australian taxa are drab monochrome brown. Apertural barriers are present in a number of species. Shell sculpture varies from strong radial costae to weak radial threads to smooth (Fig. 17.40A–D). Although the family is most diverse on high islands of the Pacific Ocean a few species live in fringing areas such as Australia (including Lord Howe Island and Norfolk Island), New Zealand and Japan. Species recorded from Mauritius and Christmas Island in the Indian Ocean were probably introduced by humans.

Cox (1864) recorded the first Australian species from Darling Point, Sydney, New South Wales. The suburban nature of this locality suggests that *Elasmias wakefieldiae* may be an introduction. Iredale (1937a, 1944a, 1945) placed the species in Elasmatinidae and Zilch (1959) included the Australian species in Tornatellinidae. However, Cooke & Kondo (1960) revised the achatinellid and tornatellid snails of the Pacific Basin and concluded that the taxa should be grouped in the single family Achatinellidae. These authors placed the Australian species in *Tornatellinops* and *Elasmias*. Solem (1988b) followed this approach in a revision of some northern Australian species, and Smith (1992) listed 12 species in two genera. However, these conclusions are not based on anatomical data and the correct generic placement of the Australian species still requires confirmation. The same or closely related genera are present in New Zealand.

Shells of the five Australian species are very small (2–4 mm in height), dextral, either ovate-conic (*Elasmias*, Fig. 17.40A) or turreted (*Tornatellinops*, Fig. 17.40D). The aperture contains a weak to strongly developed parietal barrier which varies in prominence through maturation. The columella is twisted, with or without columellar lamellae. The foot is slender, holopodous.

Nothing is known about the food preferences of the Australian species. The achatinellid jaw is mostly lacking or extremely thin when present (Pilsbry, in Pilsbry & Cooke 1912–1914). The radula consists of numerous rastriform or rake-like teeth arranged in transverse V-shaped rows. Each tooth has a long narrow basal plate with a broadened, reflected head which bears fine or broad denticles (Fig. 17.40E).

The pallial configuration is orthurethrous and consists of a long narrow kidney, tapering into a narrow, weakly differentiated ureter which leads to the pneumostome. The ureter reflexes slightly at the mantle collar edge.

Reproduction in *Elasmias* and *Tornatellinops* species is viviparous. The penis is small to vestigial and has an appendix but no epiphallus (Fig. 17.40F). Internally, there is a single recurved pilaster. The ovotestis is unilobate; the spermatheca is small with a long, narrow stalk; and embryos may be borne singly or number up to 22. Growth proceeds through a number of defined stages (Pilsbry & Cooke 1915), each marked by specific changes in shell structure. The direction of these changes, especially in adolescent growth, indicates relationships not obvious from the form of the adult shell.

The Australian species are arboreal and live in a wide range of terrestrial habitats. They have been collected from the leaves of mangrove trees, in tropical and subtropical rainforest, and in the vine thickets of eastern Queensland, northern and north-western Australia.

Whether the Australian species are accidental introductions and hence synonyms of widespread species, or whether they are true endemics, remains to be determined. *Tornatellinops* and *Elasmias* species are often found living together, but the lack of more detailed studies makes it difficult to comment on species ranges and overlap.

The family is represented in the fossil record by *Anthracopupa* (Solem & Yochelson 1979) which is recorded from the Upper Carboniferous of North America. If this interpretation is correct it indicates that a major shift in distribution of the family has taken place since the Palaeozoic.

Superfamily CIONELLOIDEA

Cionelloideans are small to large terrestrial snails that usually have a dextral shell (occasionally sinistral) which is usually ovate-conic or high-spired and turreted. The shell is either glossy and monochrome or dull with distinct colour patterns. The aperture may contain columellar lamellae. The lip is either simple or prominently thickened. The radula has a narrow, tricuspidate central tooth, the laterals are bicuspidate with a quadrate basal plate, and the marginals are multicuspidate. The ureter is recurved at the tip. An epiphallus and flagellum, or caecum, are present on the penis. The penial retractor muscle is simple and inserted on the penis. Cionelloideans are hermaphroditic, oviparous or ovoviviparous.

Two families are recognised. The Amastridae are restricted to the Hawaiian Islands. The Cionellidae are endemic to North Africa and Central Europe, but have been introduced to Australia and other parts of the world.

Family Cionellidae

This family of terrestrial snails is native to northern Europe and North America. Cionellids have small, elongate, glossy shells up to 7 mm in length. One species, *Cionella lubrica*, has been introduced into southern Australia (Smith 1992). It was first recorded in southern Western Australia by Kendrick & Sedgwick (1973) and subsequently recorded from several localities in south-eastern Australia by Smith & Kershaw (1979).

The shell is dextral, small and elongate. The aperture is ovate with a steeply sloping parietal wall, the columella is straight and the lip is not expanded or thickened within (Fig. 17.41A). These two latter characters help to separate *Cionella lubrica* from the only Australian species of the Ferrussaciidae, which is otherwise very similar. The shell is smooth and glossy and light horn-coloured. The animal is dark in colour with no peripedal groove or caudal gland.

Cionella lubrica is a detritus-feeder. The jaw is arcuate and closely plaited. The radula has few teeth; the tricuspidate central tooth is narrow, the bicuspidate laterals have a quadrate basal plate and the marginals are multicuspidate (Fig. 17.41B). The pericardium is much shorter than the kidney, which is narrowly triangular and long, and passes into a direct ureter. The pulmonary cavity has fine capillary reticulation, without visible branches in the principal pulmonary vein (Boss 1982).

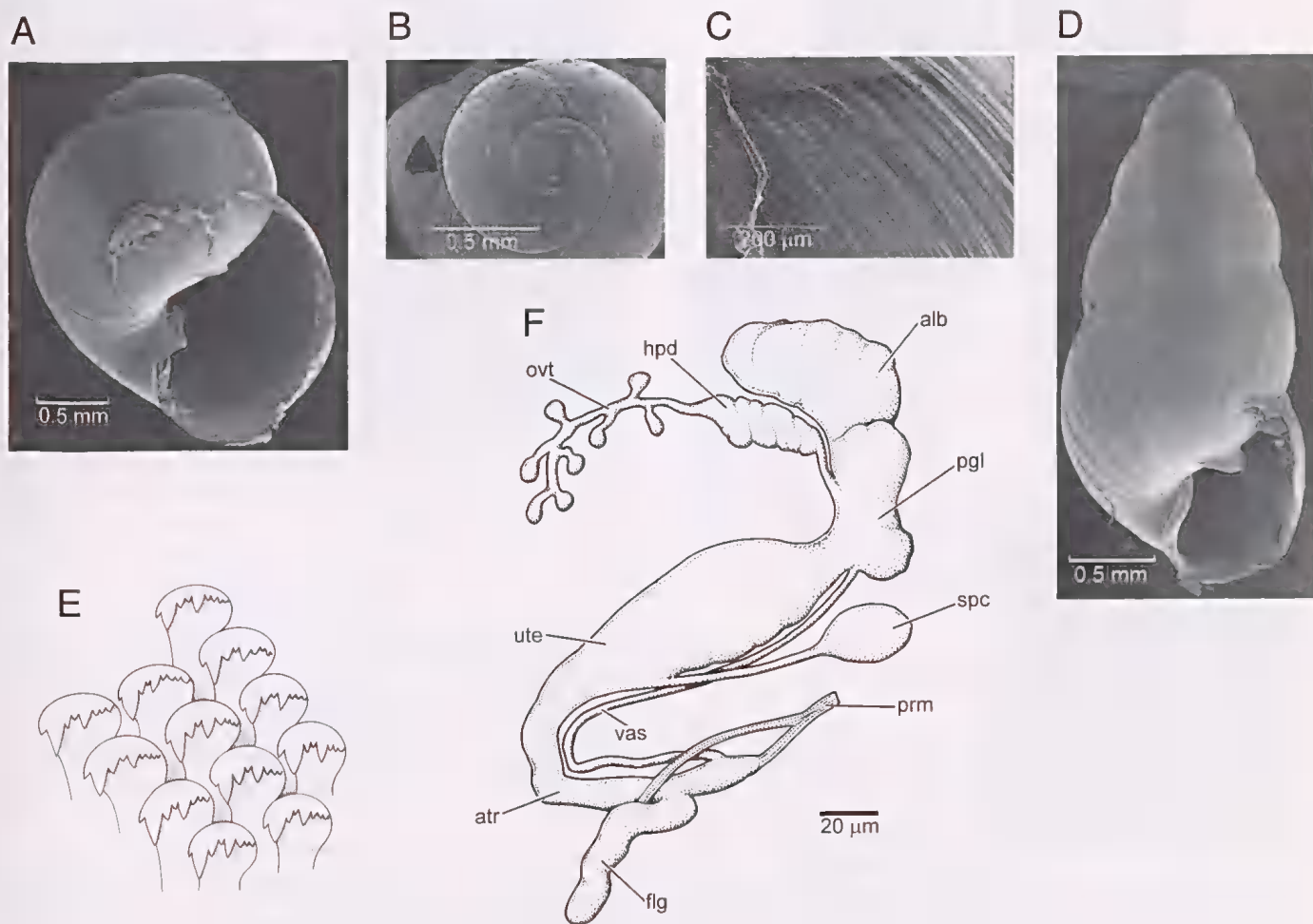


Figure 17.40 Family Achatinellidae. A–C, *Elasmias wakefieldiae*: A, shell, apertural view; B, apical shell sculpture; C, shell sculpture of a mature specimen. D, *Tornatellinops jacksonensis*, shell, apertural view. E, F, *Tornatellinops variabilis*: E, portion of radula showing some teeth which are arranged in V-shaped rows; F, reproductive tract. alb, albumen gland; atr, atrium; flg, flagellum; hpd, hermaphroditic duct; ovt, ovotestis; pgl, prostate gland; prm, penial retractor muscle; spc, spermatheca; ute, uterus; vas, vas deferens. (E, F, after Odhner 1922)

[A–D, Queensland Museum; E, C. Eadie; F, B. Scott]

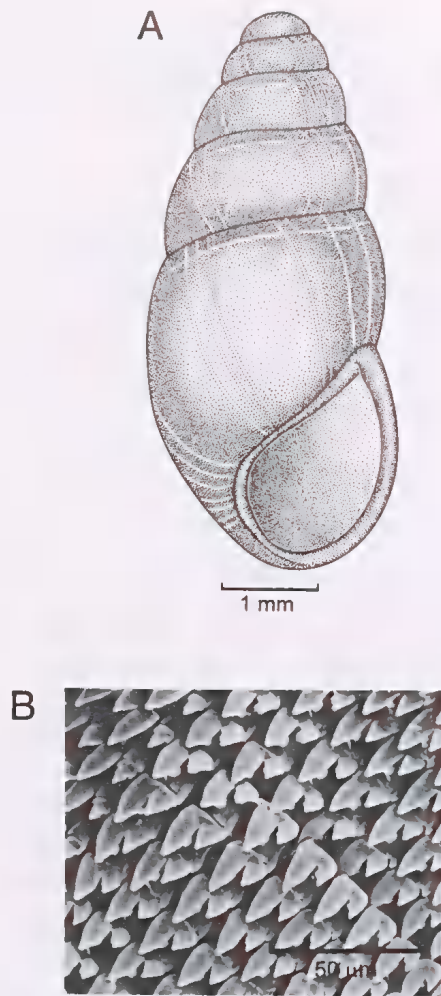


Figure 17.41 Family Cionellidae. *Cionella lubrica*: A, shell, apertural view; B, portion of radula showing lateral teeth. [A, C. Eadie; B, B.J. Smith]

Cionellids are protandric hermaphrodites. The penis has a well-developed epiphallus with a non-forked retractor muscle; a penial appendix is present.

Cionella lubrica is confined to moist, very sheltered areas in well-established gardens in a few scattered localities in southern Australia.

There is some confusion over the name by which this family should be known. Workers in Europe use the name Cochlicopidae (Kerney & Cameron 1979), but Cionellidae is used here following Pilsbry (1948) and Burch (1976b). The family contains four genera, all Palaearctic in distribution, but with one or two species introduced into various other temperate regions of the world.

Superfamily PUPILLOIDEA

Members of this superfamily are terrestrial snails with small shells that vary in shape from pupiform to elongate-turreted and subdiscoidal. The aperture is often partially occluded by one to many lamellae and denticles. The shells are usually dextral although sinistrality is common in some groups, and the lip is either sharp or thickened and slightly reflected. The radula consists of tricuspidate central and bicuspidate lateral teeth which are similar in size, and multicuspidate marginals that have a broad basal plate. The triangular kidney is tapered anteriorly and the ureter is recurved at the tip, sometimes as an open groove (Pilsbry 1948). The penis usually has an appendix and epiphallus. Pupilloideans are hermaphroditic and ovoviviparous or viviparous.

The superfamily includes four families. Of these, the Pupillidae as defined by Pilsbry (1948), is the largest; it is cosmopolitan and is represented in Australia by three subfamilies. The Strobilopsidae occur on the fringes of eastern Asia, and North and Central America. The Holarctic Valloniidae and the Euro-Mediterranean Pleurodiscidae, have been introduced into Australia.

The earliest pupilloidean has been identified from the Lower Pennsylvanian of Nova Scotia by Solem & Yochelson (1979).

Family Pupillidae

The Pupillidae are a group of very small (up to 5 mm in shell height), mainly terrestrial land snails with ovate-conic to cylindrical shells (Fig. 17.42A–H). Usually the aperture has a number of denticles and lamellae (Fig. 17.42I). Shell sculpture (Fig. 17.42L–O) consists of fine growth ridges, spiral lines, malleations and dimples. The aperture is ovate to round with a strongly reflected or simple lip. The shell is usually umbilicate.

Pilsbry (1916–1918, 1919–1920, 1920–1921, 1922–1926, 1927–1935) monographed the world pupillids and placed the Australian taxa in a global context. Although he worked with little Australian material, his approach is preferred to that of Iredale (1930, 1937a, 1937c, 1939, 1940b, 1944a, 1945) who isolated the Australian pupillid fauna taxonomically by the introduction of new taxa. Solem (1981a, 1986a) reviewed pupilloid land snails from arid areas of south, mid-west and northern Australia. Later Solem (1988b) extended his coverage to include pupillids from the Kimberley and the Northern Territory. Central and eastern Australian species have yet to be revised comprehensively. In addition to expanding distribution limits and introducing new species, Solem (1986a, 1988a) assigned the species to broader, more widespread genera (Smith 1992).

Solem (1988b) recorded a number of extralimital species in the Australian fauna for the first time. Some were merely range extensions from nearby landmasses, whereas others, such as *Gastrocopta pediculus* and *G. servilis*, were species which he considered had been introduced, probably during the 19th Century.

Dry vine thickets, open forest, strand lines and limestone outcrops are the preferred habitats of the group. Only species of *Nesopupa* occur in moist forests. Most species aestivate by sealing to objects such as rocks, leaves, the underside of logs and other shells. In contrast, *Pupisoma* species are found on the underside of the branches of trees and bushes (Solem 1988b). The shells of most species are usually covered with adherent dirt particles which can make location in the field difficult.

Shells of Australian pupillids show considerable interspecific variability in shape, sculpture and apertural dentition. *Pupisoma* species have a comparatively simple shell with an unreflected lip and no barriers (Fig. 17.42G); *Glyptopupoides egregia* has well-developed radial ribs (Fig. 17.42D) and complex microsculpture (Solem 1988b), and Australian species of *Pupoides* have a prominent angular tooth (Fig. 17.42C). The shell in *Cylindrovertilla* species is sinistral (Fig. 17.42A), as is that of *Nesopuparia norfolkensis*, which has many teeth. Shells of *Gastrocopta* and *Pumilicopta* species have many apertural barriers and a reflected lip (Fig. 17.42E, F), whereas prominent barriers (Fig. 17.42B), a reflected lip and malleated sculpture (Fig. 17.42N) are present in *Nesopupa*. *Gylittrachela* includes species of limestone-associated snails which have 'trumpet-like' apertures (Fig. 17.42H), with prominent barriers, a subperipheral sulcus and complex shell microsculpture (Fig. 17.42L–O).

Pokryszko (1996) presented anatomical data on some Australian species. Studies on extralimital pupillids have reported a radula with tricuspidate central tooth, bicuspidate laterals and multicuspidate marginals (Fig. 17.42P; Gittenberger 1973; Pokryszko 1990).

Pupillids aestivate through dry periods and produce mucoid, rather than calcareous, epiphragms. Warburg (1965) studied the water retention capabilities of *Pupoides adelaidae*. This species was

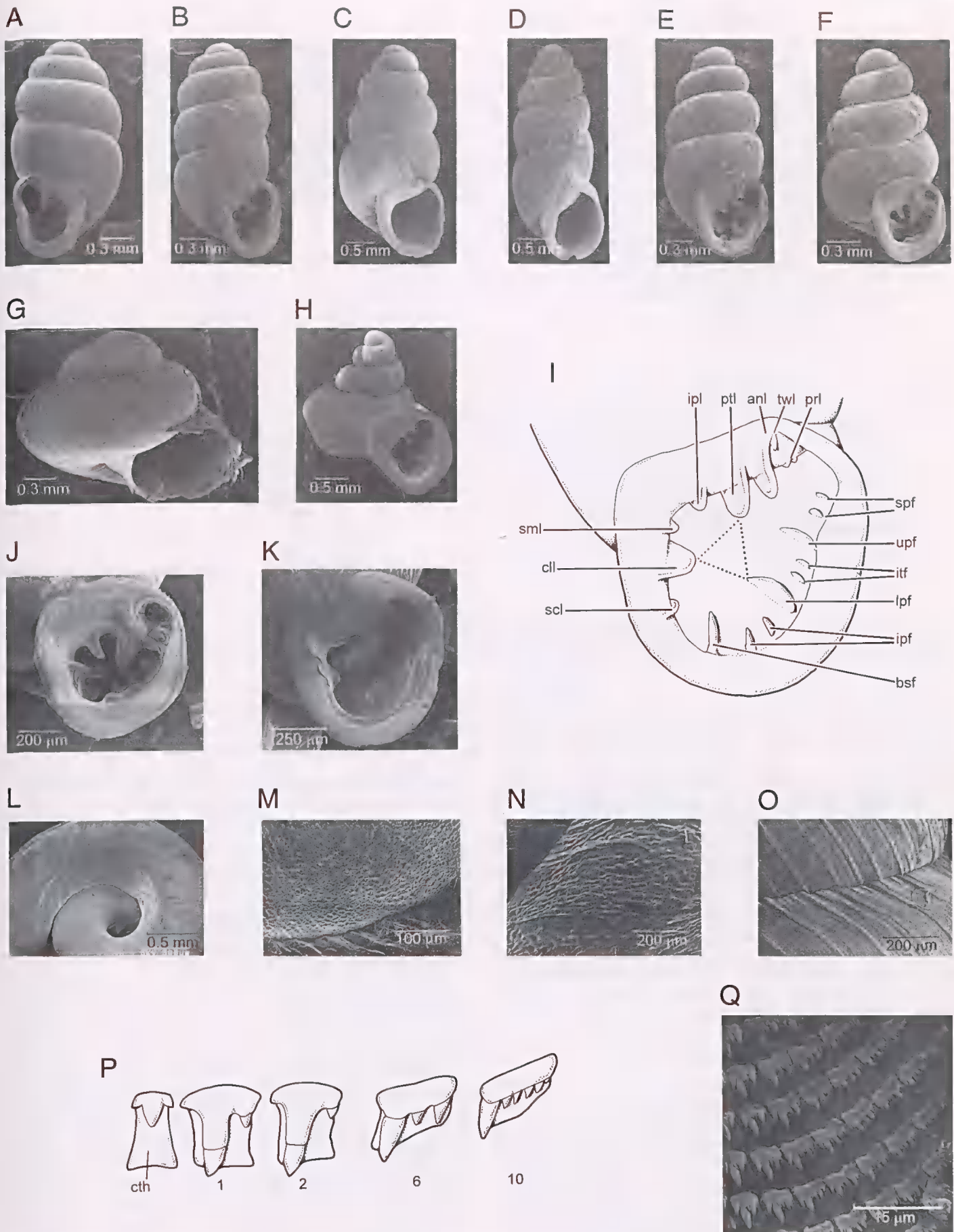


Figure 17.42 Family Pupillidae. A–H, shell forms of Australian pupillids, apertural view: A, *Cyliodactylus hedleyi*; B, *Nesopupa mooreana*; C, *Pupoides pacificus*; D, *Glyptopupoides egregia*; E, *Gastrocopta hedleyi*; F, *Pumilicopta bifurcata*; G, *Pupisoma circumlitum*; H, *Gylotricha australis*. I–K, shell apertures showing the details of apertural dentition: I, terms used to describe the apertural denticles; J, *Pumilicopta bifurcata*; K, *Nesopupa mooreana*. L–O, shell sculpture: L, *Gylotricha australis*; M, *Pupisoma circumlitum*; N, *Nesopupa mooreana*; O, *Glyptopupoides egregia*. P, Q, portions of radulae: P, half of one radular transverse row of *Gastrocopta pediculus ovatula*, a Javanese specimen; numbers denote position of tooth from the central tooth; Q, *Pupisoma orcula*, teeth on one side of the radula. anl, angular lamella; bsf, basal fold or plicae; cll, columellar lamella; cth, central tooth; ipf, infrapalatal fold or plicae; ipl, infraparietal lamella; itf, interpalatal fold or plicae; lpf, lower palatal fold or plicae; prl, parallel lamella; ptl, parietal lamella; scl, subcolumellar lamella; sml, supracolumellar lamella; spf, suprapalatal fold or plicae; twl, twin lamella; upf, upper palatal fold or plicae. (I, after Pilsbry 1916–1918; P, after Benthem Jutting 1952; Q, from Smith & Djajasasmita 1988)

[A–H, J–O, Queensland Museum; I, P, B. Scott]

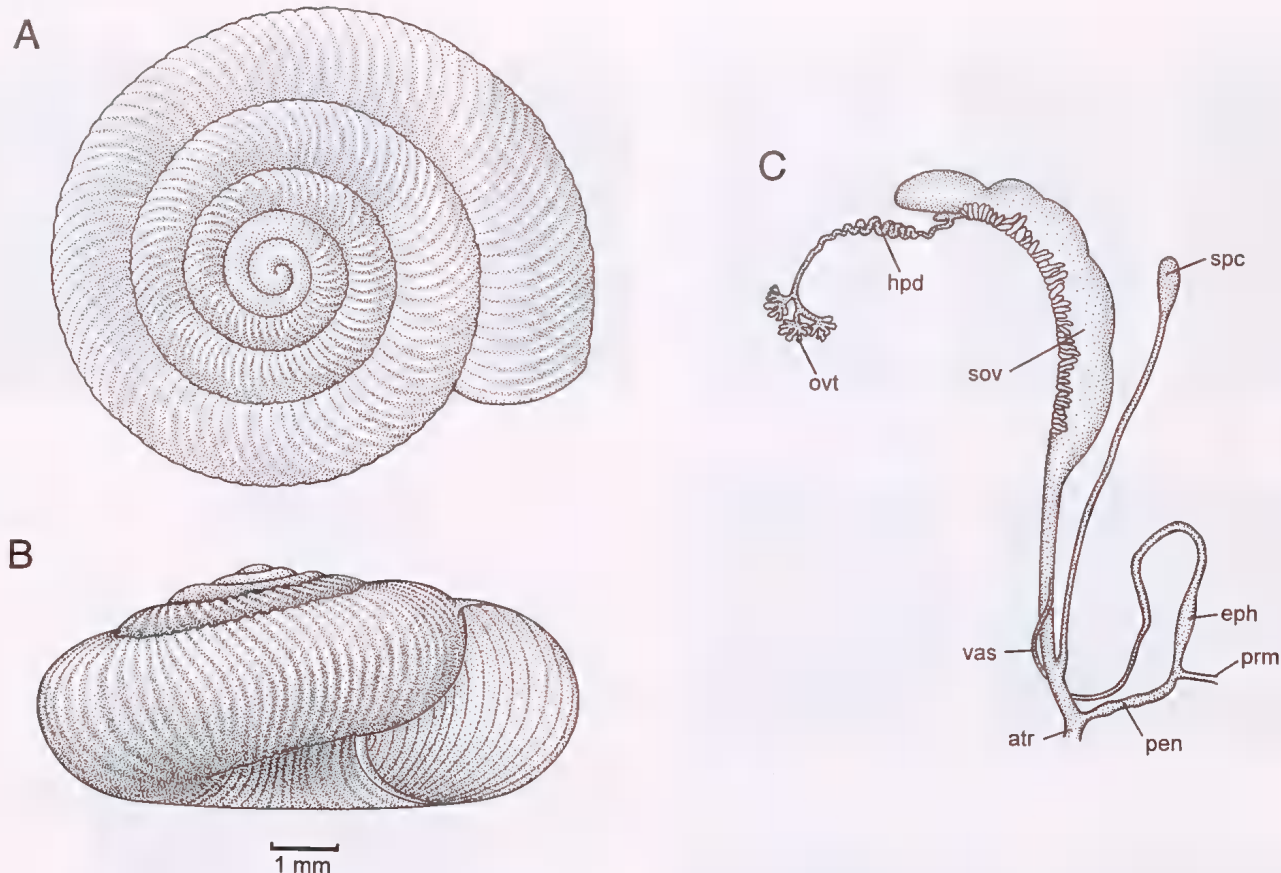


Figure 17.43 Family Pleurodiscidae. *Pleurodiscus balmei*: A, shell, apical view; B, shell, apertural view; C, reproductive tract. atr, atrium; eph, epiphallus; hpd, hermaphroditic duct; ovt, ovotestis; pen, penis; prm, penial retractor muscle; sov, spermatheca; spc, spermatheca; vas, vas deferens. (C, after Pilsbry 1927–1935)

able to survive for eight hours at 50°C. Considerable variation in shell size within populations was noted by Solem (1981a, 1986a) and presumably is related to local and seasonal conditions.

The relationships, distribution and biogeography of the Australian pupillids were briefly discussed by Solem (1986a, 1988b). Pokryszko (1996) discussed the relationships and biogeography of the Australian gastrocoptines, and concluded that this group colonised the continent on at least four occasions from Asia and the Pacific. They occur in most parts of the Australian mainland as well as Lord Howe Island, Norfolk Island and Cocos-Keeling Island. Solem (1988b) considered that only three subfamilies – Nesopupinae (*Cylindrovertilla*, *Pupisoma*, *Nesopupa*), Pupillinae (*Pupoides*, *Pupilla*, *Glyptopupoides*) and Gastrocoptinae (*Gastrocopta*, *Pumilicopta*, *Gylotrachela*) – are present in Australia. The European–Middle Eastern–North African Orculinae and the predominantly Northern Hemisphere Vertigininae are absent.

Family Pleurodiscidae

This small family of small to medium-sized land snails (5–15 mm in length) is mainly Mediterranean in distribution, but with several species extending from Europe to Japan in the Northern Hemisphere. One or two species have been known as introductions into some temperate parts of the world and a population of *Pleurodiscus balmei* has been recorded from Sydney (Shea 1982). So far the family has not been found anywhere else in Australia.

The shell is discoidal with a simple aperture, a broad umbilicus and a sculpture of ribs to fine striae (Fig. 17.43A, B). There is no colour pattern on the shell. *Pleurodiscus balmei*, in Australia, has a shell with a well-defined suture, slightly angled periphery and a sculpture of very regular, fine, sharp ribs giving the shell a sparkling appearance.

The jaw is thin and weak with flattened vertical folds. The radula has a narrow, tricuspidate central tooth, bicuspidate laterals and marginals which are pectinate and somewhat enlarged basally.

Pleurodiscids are protandric hermaphrodites and ovoviviparous. The penis is simple with no appendix or flagellum and the penial retractor inserts on the epiphallus (Fig. 17.43C).

Pleurodiscus balmei has only been found in a few localities in Sydney. It is native to southern Europe where it is found on waste ground, especially amongst rocks (Kerney & Cameron 1979). It has been introduced into several other regions of the world (Smith 1989). The family contains two genera which some authorities place in separate subfamilies or even separate families (Zilch 1959).

Family Valloniidae

Valloniids are minute to small land snails (diameter less than 10 mm) which have ovate-conic or discoidal shells. The aperture is toothless and the sculpture typically consists of fine, radial costae. The family has a Northern Hemisphere distribution extending from Europe to North America, North Africa and central Asia. Several species are known as introductions in various parts of the world. A single species, *Vallonia pulchella* (Fig. 17.44A, B) has been introduced into many parts of southern Australia, including Lord Howe Island.

The shell of *V. pulchella* is flattened and has a simple aperture and strongly reflected lip. The sculpture is smooth with occasional fine radial lines. The shell colour is white.

The jaw of *V. pulchella* is low and wide, slightly arcuate with attenuated blunt ends and consists of numerous crowded ribs (Binney 1878). The central radular tooth is tricuspidate with reduced ectocones (Fig. 17.44C). The laterals are broader than the central tooth and bicuspidate; the marginals are multicuspitate (Watson 1920).

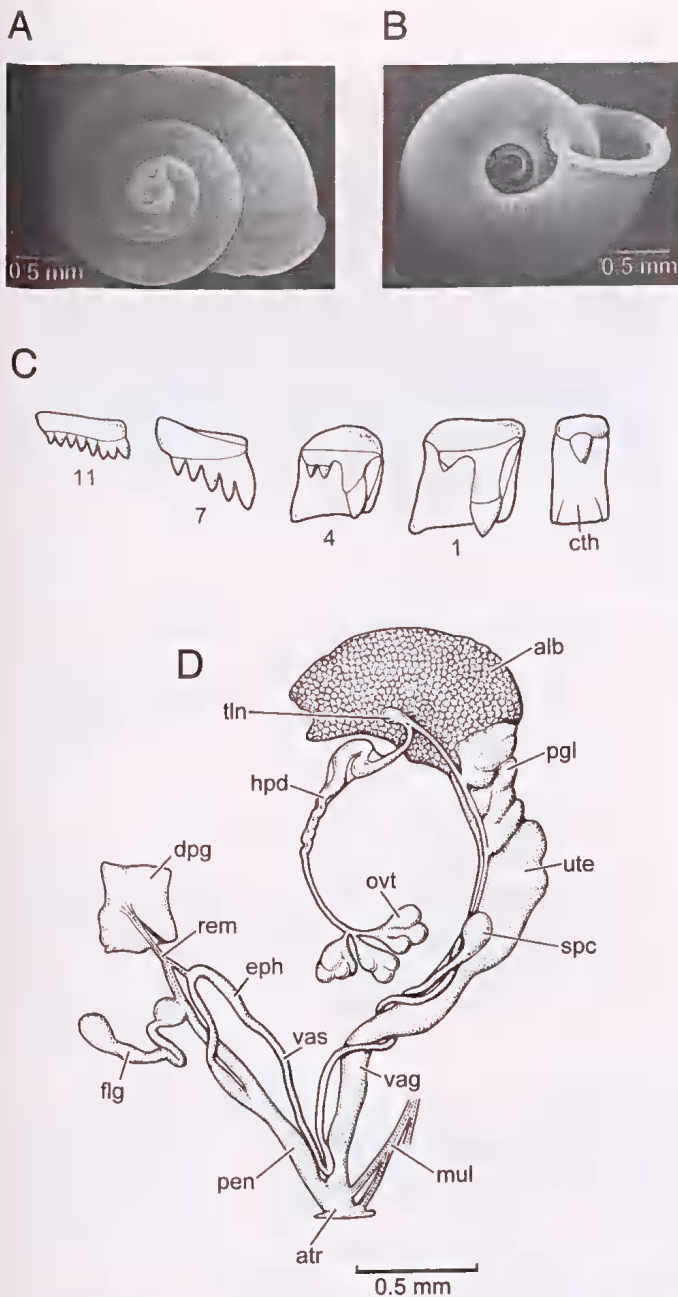


Figure 17.44 Family Valloniidae. A–C, *Vallonia pulchella*: A, shell, apical view; B, shell, ventral view; C, half of one radular transverse row; numbers denote position of teeth from the central tooth. D, *Vallonia costata*, reproductive tract. alb, albumen gland; atr, atrium; cth, central tooth; dpg, diaphragm; eph, epiphallus; flg, flagellum; hpd, hermaphroditic duct; mul, muscle; ovt, ovotestis; pen, penis; pgl, prostate gland; rem, retractor muscle; spc, spermatheca; tln, talon; ute, uterus; vag, vagina; vas, vas deferens. (C, after Watson, H. 1920; D, after Steenberg 1918)

[A, B, Queensland Museum; C, D, B. Scott]

The penis has a long appendix (Fig. 17.44D) and a divided retractor muscle (Baker, in Pilsbry 1927–35).

Vallonia pulchella is found in moist litter in suburban gardens. It feeds on decaying plant matter and is not regarded as a pest. Records of a second species, *V. costata*, from New South Wales and Tasmania (Cotton 1954) have not been confirmed and are considered erroneous (Smith & Kershaw 1979). Smith (1992) listed both species.

Literature records of the introduction of *Vallonia pulchella* are scarce although museum collections indicate that it has a widespread occurrence in temperate areas of south-eastern Australia. Petterd (1879a) recorded the species from Hobart, Tasmania, thus indicating a comparatively early introduction. Smith & Kershaw (1979, 1981) and Shea (1983) provided more recent records. The Australian populations were probably introduced accidentally from Europe.

Superfamily PARTULOIDEA

Partuloideans are ground-dwelling and arboreal terrestrial snails with ovate-conic, elongate or subcylindrical shells. The aperture may or may not have apertural lamellae and denticles. The shells are usually dextral or less commonly sinistral, coloured or drab monochrome. The lip is either sharp, or more usually, thickened and reflected. The radula has a central tricuspidate tooth, tricuspidate or secondarily bicuspidate laterals, and marginals that are tricuspidate or multicuspidate as a result of ectoconal splitting. The kidney is triangular with either a straight ureter that is recurved at the tip and opens through a lateral pore, or a pseudosigumethrous ureter (some Enidae) that opens at the pneumostome. The penis has an epiphallus which may have both a caecum and flagellum; a penial appendix may also be present. The spermatheca sometimes has a long flagellum. Partuloideans are hermaphroditic and ovoviparous.

Two families are included. The monogeneric Partulidae occurs on the high islands of the southern and western Pacific and is very diverse on the Society Islands (Crampton 1916, 1925, 1932). The two-part distribution of the Enidae consists of a basically Palearctic 'enine' group (Hesse 1933), and a more Southern Hemisphere 'cerastine' group which extends through Africa and India to Australia (Solem 1988b).

Family Enidae

Enids are characterised by shells which are usually small to medium in size, ovoid-elongate, conic or subcylindrical. The lip of the aperture is either reflected or simple and the aperture may possess one to several denticles. Australian representatives have a simple lip and barrier-free aperture.

Three species occur in Australia (Smith 1992). *Amimopina macleayi* has a conic, yellowish-brown shell and is endemic to northern Australia and southern Papua New Guinea (Fig. 17.45A). In his review of *Amimopina*, Solem (1964b) synonymised the New Guinean *A. beddomei* with *A. macleayi* from northern Queensland, and extended the range of *A. macleayi* into the Northern Territory and northern Western Australia (Solem 1988b). A second species, *Rhachistia histrio*, which has a white shell with varying degrees of dark-brown spotting and banding, is introduced (Fig. 17.45B, C). This species has been spread through the tropical Indo-Pacific and Australia by commerce (Solem 1964a). It is probably native to eastern Africa (Verdcourt 1961). The third species is also introduced: *Ena montana*, with a drab brown shell, has been recorded from Sydney (Shea 1983); it is native to Europe.

Iredale (1933) introduced the genus *Rachispeculum* for *Bulimus bidwilli*. Solem (1959a) reviewed various introduced populations of *R. histrio* and concluded that *R. bidwilli* is conspecific. Though this species occurs at various localities along the subtropical and tropical east coast of Australia, a detailed analysis of its distribution has not yet been completed.

The radulae of both *Amimopina* and *Rhachistia* are very similar (Solem 1973). The central tooth is unicuspidate with a broad spade-like cusp which is denticulate at the cutting edge. The lateral teeth are unusually bicuspidate with a secondary ectocone developed at the base of the mesocone and the marginal teeth are multicuspidate (Fig. 17.45E). Solem (1988b) inferred a possible relationship between the two groups, but Mordan (1984, 1986) suggested that the similarity in radular morphology reflects convergence in two species with specialised arboreal lifestyles.

Enids have an orthurethrous pallial configuration. However, a number of species, including *A. macleayi* and *R. histrio*, display pseudosigumethrous conditions (Fig. 17.45D) in which folds of the pallial roof (renal and rectal folds) form a structurally open, yet functionally closed, sigumethrous ureter (Solem 1964b).

Some enids are ovoviparous, but the situation in *A. macleayi* and *R. histrio* is not known. The enid reproductive system is characterised by accessory appendages on the male genitalia (Fig. 17.45F). In *A. macleayi* and *R. histrio* a penial appendix with

17. PULMONATA

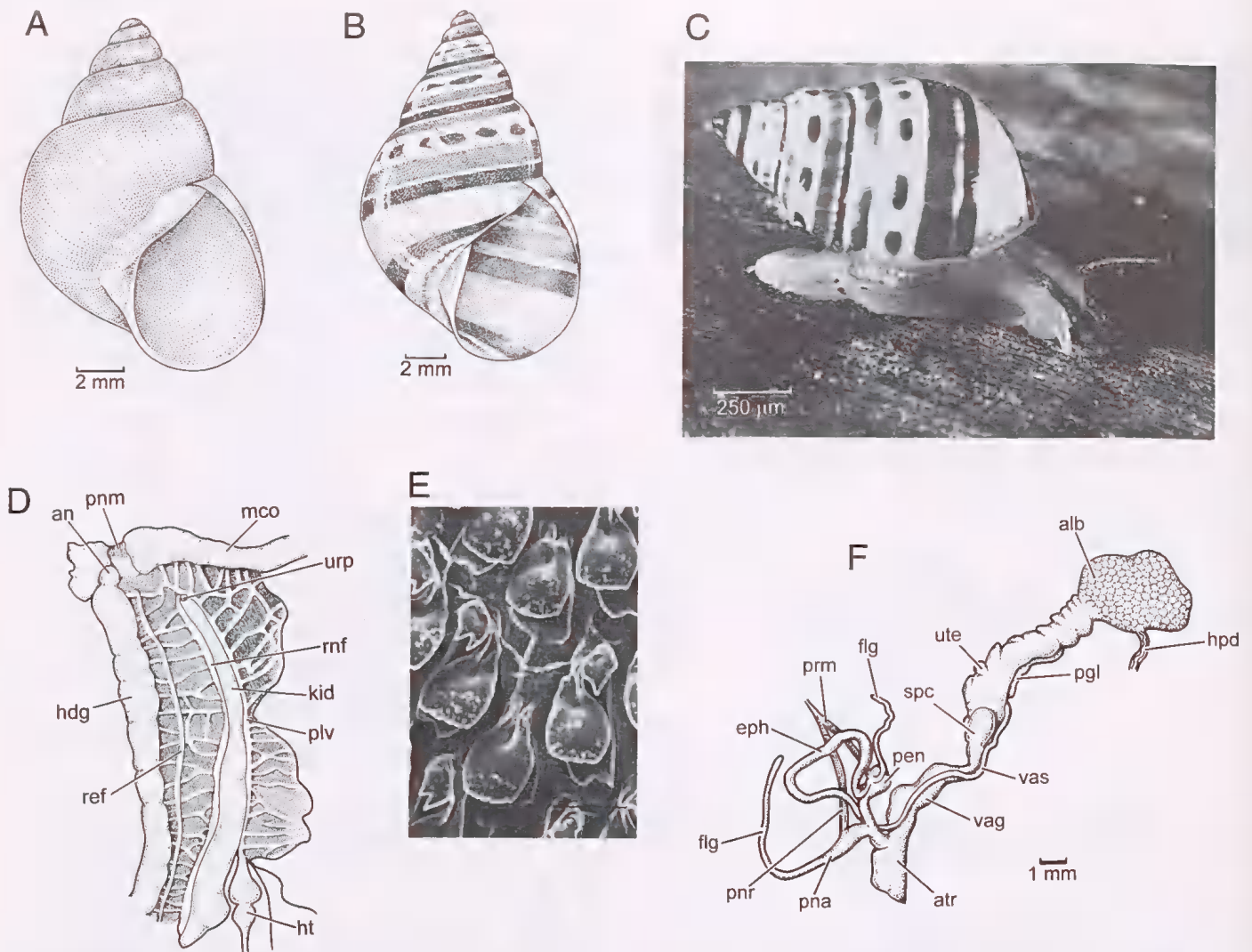


Figure 17.45 Family Enidae. **A, B**, shells, apertural view: **A**, *Amimopina macleayi*; **B**, *Rhachistia histrio*. **C**, *Rhachistia histrio*, crawling animal. **D**, *Amimopina macleayi*, pallial configuration. **E**, *Rhachistia histrio*, portion of radula showing central teeth. **F**, *Amimopina macleayi*, reproductive tract. **alb**, albumen gland; **an**, anus; **atr**, atrium; **eph**, epiphallus; **flg**, flagellum; **hdg**, hindgut; **hpd**, hermaphroditic duct; **ht**, heart; **kid**, kidney; **mco**, mantle collar; **pen**, penis; **pgl**, prostate gland; **plv**, pulmonary vein; **pna**, penial appendix; **pnm**, pneumostome; **pnr**, penial appendix retractor; **prm**, penial retractor muscle; **ref**, rectal fold; **rnf**, renal fold; **spc**, spermatheca; **urp**, ureteric pore; **ute**, uterus; **vag**, vagina; **vas**, vas deferens. [A, B, R. Plant; C, E, Queensland Museum; D, F, B. Scott]

a long flagellum and an epiphallic flagellum are present. The atrial cavity, and to some extent the vagina, are lined with brown, spongy tissue. The spermatheca does not have a stalk.

The Australian species are arboreal. However, more usually members of the family are ground-dwelling. Solem (1988b) concluded, on the basis of material collected from north-western Australia, that individuals become reproductively active only in their third wet season.

Mordan (1984) has demonstrated that two lineages are involved in the traditional concept of the family Enidae. Palearctic genera, the 'enine' group, are anatomically distinct from the more southern Cerastuinae. Genera of the latter subfamily are thought to be of Gondwanan origin (Solem 1988b). *Amimopina* and *Rhachistia* belong to a group of cerastine genera also distributed in Madagascar, India and Sri Lanka.

Solem & Yochelson (1979) assigned *Dendropupa* from the late Palaeozoic of Canada and Poland to the Enidae. Although this established the antiquity of the family, the overall fossil record of the group is sparse and scattered (Mordan 1984).

Infraorder SIGMURETHRA

Sigmurethrans are minute to very large-sized snails with spirally coiled shells which are extremely variable in shape. The shells are usually dextral, though sinistral forms predominate in a few groups. Lamellae and denticles are usually absent from the aperture. In some groups the shell is secondarily reduced or

completely absent. The kidney is variable in shape. The reflexed ureter passes to the posterior end of the lung cavity, turns across to the last fold of the gut and follows it forward to the mantle edge as an open groove or closed tube (Pilsbry 1900a). The foot is either holopodous (pedal grooves inconspicuous or close to the angle of the foot) or aulacopodous (pedal groove situated well above the lateral angle of the foot).

The condition of the foot has led authors (Pilsbry 1946; Solem 1978a; Smith 1992) to partition the Sigmurethra into three subgroupings – the Aulacopoda, Holopoda and Holopodopes. The first two groups are based solely on the position of the pedal groove whereas the latter was proposed by H.B. Baker (1955, 1962) for species with a heterourethrous kidney. In such kidneys, the initial part of the ureter runs transversely along the kidney to the rectum before reflexing toward the pneumostome. This contrasts with the more widespread condition in which the ureter firstly reflexes posteriorly before again reflexing to follow the rectum anteriorly. The Holopodopes included taxa with either an aulacopodous or holopodous foot. These divisions are not adopted here and the Sigmurethra is divided into superfamilies following Solem (1978a). Tillier (1989) proposed a marked re-organisation of families within more traditional superfamily groupings. Nordsieck (1992) divided the Sigmurethra into four infraorders, the Clausilionei, Succineoinei, Achatinoinei and Arionoinei. These arrangements have yet to achieve more wide-spread acceptance.

The fossil record of the Sigmurethra dates from the late Palaeozoic of the Northern Hemisphere (Solem & Yochelson 1979).

Superfamily ACHATINOIDEA

Achatinoids are small to very large-sized snails that have a shell which varies in shape from pupiform to elongate-turreted or ovate-conic, and rarely, subdiscoidal. Sculpture consists of weak to prominent radial ribs or is absent. The aperture sometimes contains one to several lamellae. The foot is usually holopod without peripodal grooves. The jaw is reduced or absent. The radula tooth rows have a narrow unicuspidate central tooth, lateral teeth that are either bicuspidate or tricuspidate, and usually multicuspidate marginals. The long, tapered kidney is approximately triangular. Some species have a simple reproductive system. The penis may or may not have an epiphallus and accessory appendages. Some achatinids, and probably the megaspirids are oviparous, and ovoviviparity is common in some groups.

Five families are included in the superfamily. Only one of these, the Spiraxidae from the Americas, is not present in Australia. A single relict species of the Megaspiridae is present; the family is otherwise known from Brazil and New Guinea. The Subulinidae, basically a West Indian group, are represented by several endemic and several introduced species, and the mainly Mediterranean Ferrussaciidae by a single introduced species. The family Achatinidae was represented in the fauna through the introduction of *Achatina fulica* in the early 1970s, but this species has since been eradicated.

Family Ferrussaciidae

This family of elongate, glossy snails is native to Europe and Asia. One introduced ferrussaciid, *Ferrussacia folliculus*, has been recorded from South Australia (Cotton 1954). Though the species appears to be established in some suburban gardens in Adelaide it has not been found anywhere else in Australia. Additional information concerning this species was given by Venmans (1957).

The shell is dextral, small (10 mm in length) and elongate, with a rounded to pyriform aperture and a small, smooth, pointed apex (Fig. 17.46). The peristome is sometimes thickened within and the columella is basally truncate or incurved. These two features differentiate it from cionellids with which it might be confused. The shell is glossy, almost transparent and light horn-coloured. The suprapedal groove is well developed in *F. folliculus* and the edge of the foot is fimbriate.

Ferrussacia folliculus is a detritus feeder. The jaw is thin, striated with parallel grooves, and curved. The achatinoid radula bears a very small, straight, unicuspidate central tooth, bicuspidate or tricuspidate laterals and marginals with denticulations. The ducts of the salivary glands are short. The kidney is long, transverse and tapered anteriorly and the ureter is long.

Ferrussaciids are protandric hermaphrodites and are ovoviviparous. The penis has a glandular appendix.

There is some confusion over the spelling of this family name. The usage here is derived from the genus name *Ferrussacia*. It is based on a misspelling of Férussac.

Family Subulinidae

Members of the family Subulinidae are terrestrial litter dwellers. All Indo-Pacific taxa have multi-whorled, usually slender and very elongate, greasy white to light yellow horn-coloured shells that are, with few exceptions, 5–25 mm in height (Fig. 17.47A–E). In all species found in Australia, the columella is solid and without either plicae or ridges, and varies from truncate to continuous with the shell lip. The animal is yellow or yellow-orange in colour. Usually adults have several large, white, encapsulated eggs in the uterus that are visible through the last whorl of the shell. All species have a generalised jaw and radula (Fig. 17.47F).

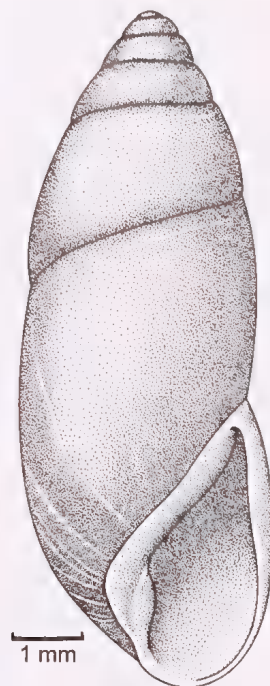


Figure 17.46 Family Ferrussaciidae. *Ferrussacia folliculus*, shell, apertural view. Introduced from Europe, it has only been found in some Adelaide gardens. [C. Eadie]

The only comprehensive monograph is that of Pilsbry (1905–1906). Subsequent studies have been regional. Data on modified generic concepts are widely scattered and mostly uncollated. Many species have been introduced throughout the tropics by humans and then mistakenly described several times as endemics, compounding the confusion. Australia has two native species, three confirmed introductions, and quite probably additional introduced species (see Solem 1988b, 1989). Smith (1992) listed two endemic and three introduced species.

Subulinids inhabit a wide variety of vegetation types, from synanthropic areas such as city gardens, parks, roadside debris, plantations, and pastures, to natural areas. The latter vary from rainforest patches in the Kimberley, Northern Territory, Queensland and New South Wales, to litter beneath fig trees or exposed talus heaps in arid central Australia. Subulinids are generalised plant or detritus feeders, without modified radular teeth. No feeding specialisations have been reported for any of the widely distributed species.

Some evidence exists that they will be attacked by predatory snails, such as the introduced *Gulella bicolor*, but not to the extent that it could be used as a biocontrol agent.

No studies on the reproduction of Australian taxa have been published. Presumably they are protandrous hermaphrodites. They are ovoviviparous, since adult specimens normally have several eggs with calcareous shells present inside the uterus. Very few data are recorded on the anatomy of either native or introduced species (Fig. 17.47G, H; Solem 1988b). Their lifespan is unknown.

The native subulinids aestivate through the dry months, secreting up to twelve calcified sheets of mucous epiphragms across the shell aperture and adjacent portions of the last whorl to retard water loss. The introduced taxa are restricted to wetter areas and secrete only mucoid epiphragms.

Sometimes the introduced species become minor pests in gardens or nurseries, eating holes in the leaves of cultivated plants, but they do not cause major problems.

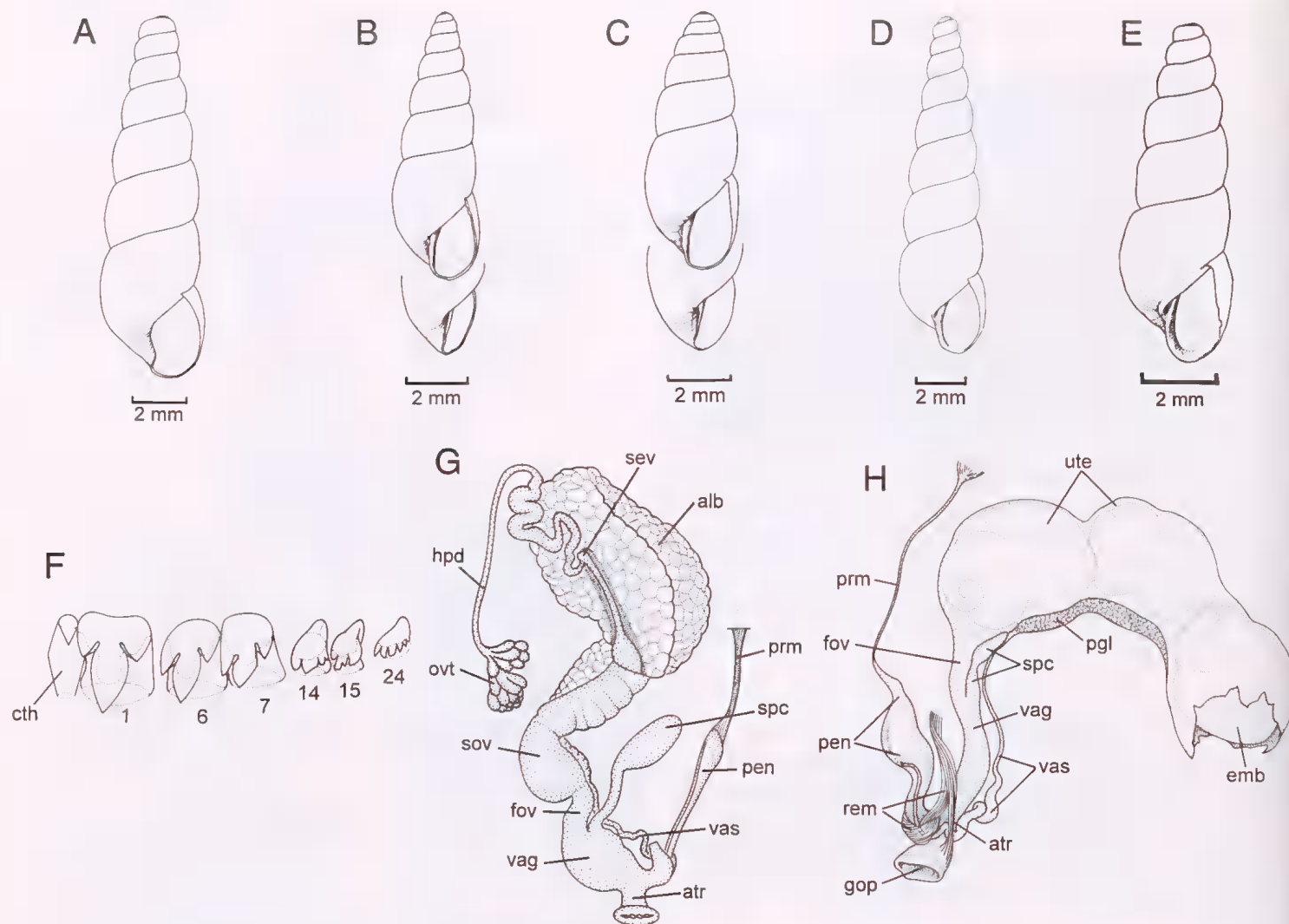


Figure 17.47 Family Subulinidae. A–E, apertural views of the characteristically elongate subulinid shells: A, *Subulina octona*; B, *Lamellaxis gracilis*; C, *Lamellaxis clavulinus*; D, *Eremopeas interioris*; E, *Eremopeas tuckeri*. F, G, *Lamellaxis clavulinus*: F, half of one radular transverse row, numbers denote position of tooth from the central tooth; G, reproductive tract. H, *Eremopeas interioris*, reproductive tract. alb, albumen gland; atr, atrium; cth, central tooth; emb, embryo; fov, free oviduct; gop, gonopore; hpd, hermaphrodite duct; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; rem, retractor muscle; sev, seminal vesicle; sov, spermoviduct; spc, spermatheca; ute, uterus; vag, vagina; vas, vas deferens. (D, E, H, after Solem 1989; F, G, after Pilsbry 1946) [A–E, A. Solem; F–H, C. Eadie]

Approximately 42 genera have been referred to this family. The one Australian endemic genus comprises two species: *Eremopeas interioris* occurs from the Pilbara and Kimberley of Western Australia, through much of central Australia; and *E. tuckeri* from the Northern Territory above the Roper River, then east to Torres Strait and south to Narrabri, New South Wales (see Solem 1988b). The 'tropical tramp' species, *Lamellaxis gracilis* and *L. clavulinus*, and *Subulina octona*, were introduced into Australia, before 1863 and 1900, respectively. All are well-established members of the Australian fauna, and inhabit both native and disturbed habitats (Solem 1988b). *Lamellaxis clavulinus* replaces *L. gracilis* whenever the two species become sympatric (Solem 1989). Other subulinid species that were widely introduced and have become well established throughout the Pacific Basin, such as *Opeas pumilum* and *Prosopeas achatinaceum*, are probably already, or soon will be, present in Australia (see Solem 1989).

Dead animals that have lost their surface sculpture are almost impossible to identify, and juveniles also cause confusion.

Family Megaspiridae

Megaspirids form a small family of terrestrial land snails with high-spined, turreted or cylindrical shells that can attain 70 mm in height. The whorls are coiled about a hollow or, at least, perforate axis. The shell may be umbilicate or imperforate, and is usually dextral, rarely sinistral. The aperture is small, ovate, with columellar and often parietal lamellae. The shell sculpture consists of fine radial ribs.

A single species, *Coelocion australis*, occurs in Australia (Smith 1992). Other megaspirids are found in New Guinea (*Perrieria*) and Brazil, South America (*Callionepion* and *Megaspira*). *Coelocion australis* has been variously referred to the Clausiliidae (Forbes 1851) and the Subulinidae (Fischer 1887). Hedley (1892) referred *C. australis* to the sinistral New Guinean *Perrieria* in the Megaspiridae. Pilsbry (1904) followed Hedley's classification but placed the species in a new subgenus, *Coelocion*. Iredale (1937a) elevated *Coelocion* to generic status and placed the species in its own family, the Coelociontidae. However, until the relationships of *C. australis* are studied in detail, retention in the Megaspiridae is desirable (Burch 1976a).

Comprehensive anatomical studies of *Coelocion australis* have yet to be undertaken. The species is not well represented in museum collections even though its relatively wide distribution has been known for some time (Hedley 1892; Pilsbry 1904). Fischer (1883) provided some data on the dentition of *C. australis* and Pilsbry (1904) presented a detailed account of its shell. *Coelocion australis* is characterised by a long cylindrical shell with numerous whorls (Fig. 17.48A) and is often decollate (with apical whorls discarded). The sculpture consists mainly of prominent radial ribs (Fig. 17.48B, C). The periostracum is a dull, dirty yellow-green colour which gives the incorrect impression that the animal has been dead for some time. The animal colour is bright lemon-yellow, similar to that of some subulinids. *Coelocion australis* has one parietal and two columellar lamellae (Fig. 17.48D). The latter are sometimes not visible from the aperture. Size differences in the shells of different populations,

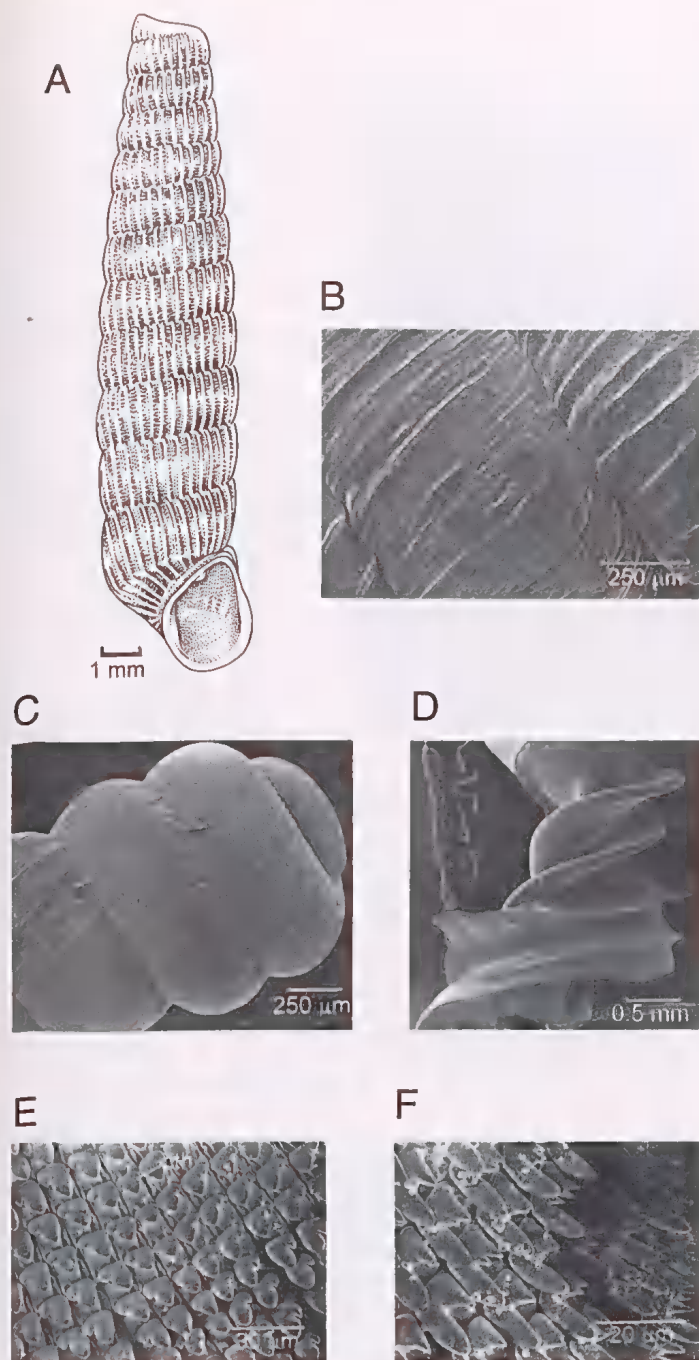


Figure 17.48 Family Megaspiridae. *Coelocion australis*, confined to the wet forests of Queensland, is the only megaspirid in Australia. A, shell, apertural view; B, adult shell sculpture; C, protoconch; D, internal lamellae; E, portion of radula showing central and lateral teeth; F, portion of radula showing marginal teeth. [A, R. Plant; B–F, Queensland Museum]

noted by Pilsbry (1904), may be due to local and seasonal variation in the environment or to the presence of more than a single species.

The radula of *C. australis* has a central tooth with a single wide cusp. The laterals are bicuspidate with a short ectocone (Fig. 17.48E) and the marginals are multicuspidate with an ectocone which is split into a number of tiny cusps (Fig. 17.48F). A transitional zone of teeth with a large mesocone and bifid ectocone is present between the laterals and marginals. The jaw is arcuate and almost smooth, with traces of vertical striae (Pilsbry 1904).

Megaspirids are probably oviparous. The penis of the male has an elongate diverticulum, and the female genitalia lack accessory ducts and sacs (Pilsbry 1904).

Coelocion australis has a disjunct distribution between Proserpine, mid-eastern Queensland, and Mt Mee, south-eastern Queensland. It lives in the litter among rocky talus in the coastal

and subcoastal vine forests and thickets. The affinities of the Australian species cannot be accurately determined until detailed anatomical studies are completed. However, the relict nature of megaspirid genera has been the subject of comment by Pilsbry (1904), Solem (1959b) and Bishop (1981).

The family has no fossil history in Australia although a fossil megaspirid has been documented from the Upper Cretaceous of Europe (Zilch 1959; Pilsbry 1904).

Family Achatinidae

Achatinidae are a family of snails with large to very large shells (from 20–230 mm in height) which are usually ovate-conic, rarely cylindrical, and have variable colour patterns. Coiling is usually dextral, rarely sinistral. The shell is imperforate, sometimes scarcely umbilicate.

The family is indigenous to the African continent and some off-lying islands but the giant African snail, *Achatina fulica*, has been introduced into North America, many Indo-Pacific islands, Hong Kong and elsewhere in Asia. It is especially significant as a pest of domestic crops. In 1977, a population of *A. fulica* was discovered at Gordonvale, near Cairns, North Queensland (Colman 1977). Subsequent eradication procedures appear to have completely eliminated the species from the Gordonvale area, however, monitoring continues. Specimens of *A. fulica* are occasionally discovered by quarantine officers in containers and holds of transport ships and reintroduction is a distinct possibility.

Mead (1961) presented a significant treatise on the giant African snail and its economic importance, and provided a valuable and comprehensive list of references on this species.

The shell of *A. fulica* is narrowly conic (Fig. 17.49A), and is up to 200 mm in length though the average is 50–100 mm. The shell colour is variable but usually consists of alternating brown and cream (or white) bands. The body is brownish-grey in colour and may be up to 300 mm in length when fully extended.

The achatinid jaw striated (Fig. 17.49C), and the radula has tiny central teeth each with a small to minute cusp which may be denticulate (Fig. 17.49D). The laterals may or may not have an ectocone and are either bicuspidate or tricuspidate. The marginal teeth are similar to the laterals. The central cusp on the marginals and laterals may be large and broad. The kidney is two to three times the length of the pericardium. The reproductive system is relatively simple (Fig. 17.49E, F) and has no accessory structures (Mead 1950; Benthem Jutting 1951). *Achatina fulica* reaches sexual maturity at 5–9 months depending on food availability and environmental conditions. The average snail can lay up to 1000 eggs in a lifetime and the normal clutch size varies from 40 to 200 eggs (Fig. 17.49B). The incubation period is 8–21 days depending on ambient conditions (Meer Mohr 1949; Pawson & Chase 1984). Eggs are ovate to spheroid, 4.5–5.5 mm in diameter.

Its size, voracious appetite and catholic diet, make *A. fulica* one of the most economically significant terrestrial pulmonate pests. According to Watson (1985), *A. fulica* is known to consume over 500 different plant species. Among the preferred plants are such commercially significant species as papaya, cocoa, and most legumes and cucurbits.

In the last 150 years this snail has spread, with human help, from Africa to Mauritius, the Indian subcontinent, the Indo-Malay Archipelago, Papua New Guinea, the Philippines, Hong Kong, Caroline Islands, Vanuatu, New Caledonia, the Society Islands, and Hawaii and Florida in the United States of America. Many of the early introductions were probably accidental with juvenile snails being transported on plant material. During World War II the Japanese introduced *A. fulica* to Guam, the Philippines and other Pacific Islands as an extra food source for soldiers. More recently tourists and travellers have become significant agents in the spread of this snail. Its large size and unusual appearance makes *A. fulica* an attractive souvenir.

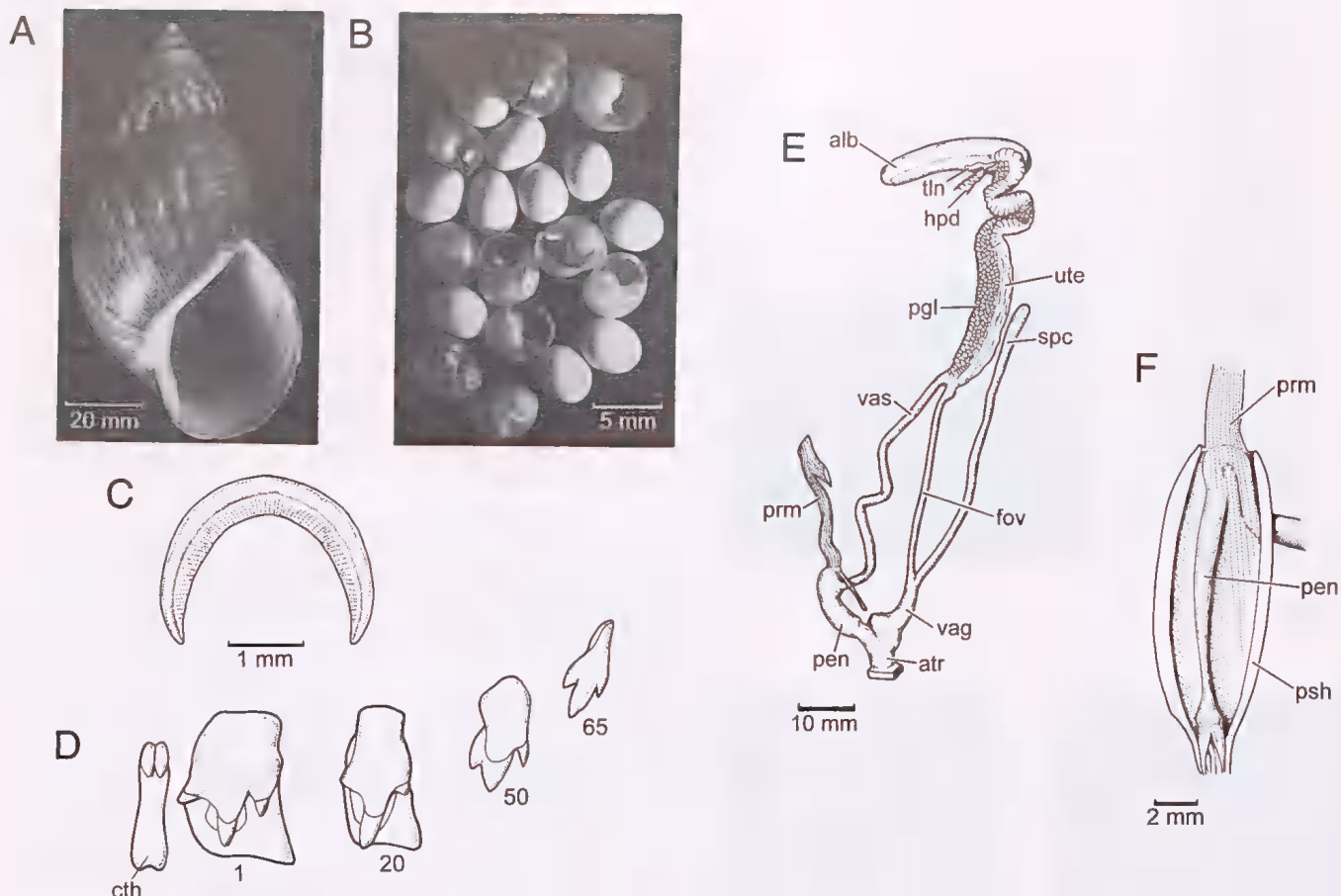


Figure 17.49 Family Achatinidae. *Achatina fulica*, the giant African snail, is prohibited from entry into Australia. A, shell, apertural view; B, eggs and hatchlings; C, jaw; D, half of one radular transverse row, numbers denote position of tooth from central tooth; E, reproductive tract; F, details of copulatory organ. alb, albumen gland; atr, atrium; cth, central tooth; fov, free oviduct; hpd, hermaphrodite duct; pen, penis; pgl, prostate gland; prm, penial retractor muscle; psh, penis sheath; spc, spermatheca; tln, talon; ute, uterus; vag, vagina; vas, vas deferens. (C, D, after Benthem Jutting 1951; E, F, after Mead 1950)

[A, B, Queensland Museum; C–F, B. Scott]

Eradication procedures are difficult to implement once the snail has colonised local forests. In the Gordonvale outbreak the population was sufficiently delimited at the time of discovery to enable hand collecting, fumigation and baits to be used for effective control. Biological control by the way of introduced predatory carnivorous snails (notably *Euglandina* species) has been attempted on several of the Pacific Islands. Unfortunately this has had disastrous results for the native snail fauna and has had little if any significant impact on *A. fulica* (see Colman 1977).

Achatina fulica has been implicated as a vector of the rat lungworm *Angiostrongylus cantonensis*. This nematode can cause parasitic meningoencephalitis in man (Malek & Cheng 1974) and at least one such case has been documented (Watson 1985).

Superfamily STREPTAXOIDEA

The small to medium-sized shells of streptaxoidean snails are relatively variable and sometimes irregularly coiled. The aperture frequently has lamellae and denticles. The lip may be simple or thickened. The central tooth of the radula is unicuspidate, reduced or absent and the lateral teeth are dagger-like and arranged in V-shaped rows. There is no jaw (Tryon 1885). The kidney is broad. The reproductive system is relatively simple, although the penis has an appendix (Pilsbry 1919). Streptaxoideans are hermaphroditic, ovoviviparous or oviparous (Benthem Jutting 1950). There is a single family, the Streptaxidae.

Family Streptaxidae

Streptaxids are carnivorous land snails that feed on a variety of invertebrates including other snails. Most have colourless shells that vary in shape from helicoid and ovate-conic to pupiform (Fig. 17.50A), cylindrical or subdiscoidal. Coiling is often irregular. The shell is small to medium-sized, rarely attaining 50 mm in height.

Shell sculpture varies from smooth to prominently, radially ribbed (Fig. 17.50B). The shell aperture may have teeth or lamellae (Fig. 17.50C). The lip is thickened or reflected. The radula is narrow and long, with or without central teeth; the lateral teeth are numerous, dagger-shaped and arranged obliquely (Fig. 17.50D). The animal is brightly coloured.

The Streptaxidae are common in Africa, South America and mainland Asia (Bruggen 1967). The family contains over 90 genera and 600 species. Stanicic (1981a) recorded the introduced species, *Gulella bicolor* from the Northern Territory. *Streptostele musaecola* has been introduced into the Polynesian–Melanesian region from West Africa and may be found in tropical Australia in the future (Solem 1988b).

Gulella bicolor has an elongate, relatively smooth shell (Fig. 17.50A), the sutures edged with short ribs (Fig. 17.50B). The aperture has a large columellar barrier; and a small basal, a very large outer palatal, and a prominent parietal barrier are also present (Fig. 17.50C). *Streptostele musaecola* is slightly smaller, has radial ribs which are also prominent on the whorls, and lacks apertural barriers (Solem 1988b). Animals of both species are red.

Little is known of the anatomy of this family. The penis is armed with spines and has a sheath. Streptaxids are either ovoviviparous or oviparous (Benthem Jutting 1954), and the eggs are comparatively large and few in number.

Most streptaxids live in the litter or under stones and logs. Malaysian species are almost exclusively associated with limestone hills (Benthem Jutting 1954). *Gulella bicolor* is a circum-tropical tramp species. It was described from India but its geographical origin is uncertain (Naggs 1989). In Darwin, Northern Territory, the species is common in local gardens but has yet to be found in native bush.

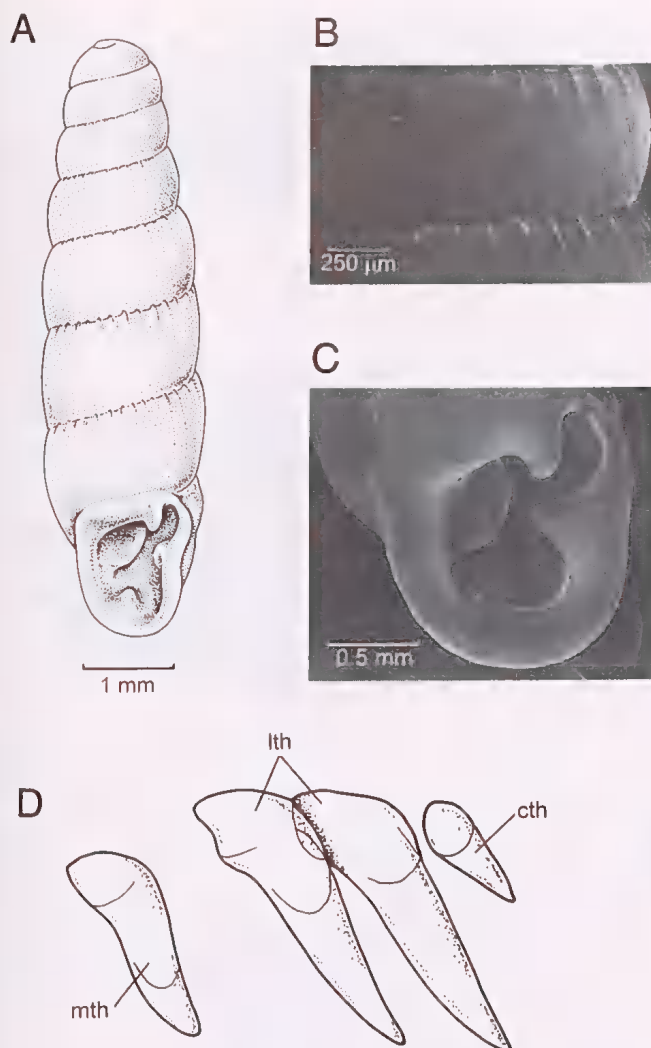


Figure 17.50 Family Streptaxidae. *Gulella bicolor*, an introduced species, is found along the coast of the Northern Territory. A, shell, apertural view; B, portion of shell showing adult sculpture and a suture; C, aperture showing the apertural barriers; D, some teeth from a half radular transverse row showing the small central tooth, two large lateral teeth and one large marginal tooth. cth, central tooth; lth, lateral teeth; mth, marginal tooth. (D, after Benthem Jutting 1950) [A, R. Plant; B, C, Queensland Museum; D, B. Scott]

Gulella bicolor is a predator of other snail species, among them subulinids and pupillids. In the Northern Territory, it has been observed preying on the introduced subulinid, *Subulina octona* (see Solem 1988b). Dundee & Baerwald (1984) present information on reproductive habits, population structure and food preferences based on observations of an introduced population in Louisiana, United States of America. The impact of these carnivorous introduced snails on Australian native species has not been assessed but the potential exists for considerable damage to the local snail fauna if they invade native forests.

Superfamily RHYTIDOIDEA

Rhytidoideans are mainly carnivorous snails in which the jaw is usually absent, rarely vestigial. The shell varies in shape from depressed helicoid to discoidal. In some taxa, it is auriform or reduced to small internal plates. The shell is usually not strongly calcified, and the aperture only rarely contains lamellae. The foot is usually holopodous although peripodal grooves are present in some groups. The radula has reduced or absent central teeth and large, dagger-like lateral and marginal teeth. The kidney is long, subtriangular and usually lacks a secondary ureter. Rhytidoideans are either oviparous or ovoviviparous. The penis generally has an epiphallus.

Five families are included – the Haplotrematidae from North, Central and South America; the monotypic Macrocyclidae from Chile; the small-sized Systrophiidae from South America; the slug-like Aperidae (= Chlamydephoridae) from South Africa; and the widespread, southern Rhytididae (= Paryphantidae). The latter family is the only one present in Australia.

The superfamily has a poor fossil record. However, the Rhytididae are represented in Pliocene deposits in New Zealand (Solem 1979a).

Family Rhytididae

Rhytidids are carnivorous terrestrial snails (Figs 1.65, 17.20E; Pl. 31.3) with Gondwanan distributions. They occur in eastern and southern Australia, New Zealand, islands of the western Pacific including New Caledonia, and also the Seychelles and South Africa (Smith 1984). The shell varies from small to very large (2–140 mm in diameter) and is subglobose to discoidal in shape. It is usually thin with reduced calcareous elements and is composed mainly of conchin (Fig. 17.51A–D). Ten of the 22 genera in the family occur in Australia. Many of the 25 Australian species (see Smith 1992) have little or no sculpture; in some the sculpture comprises simple, more or less prominent radial ribs. In the Australian species, the colour of the shell varies from light-yellow through dark-honey to black; colour patterning is rare, unlike some species from New Zealand and the South Pacific.

In Australia the first species were collected by early French expeditions and described by Férussac in 1832. Iredale (1933, 1938, 1943c) reviewed the family and introduced many new generic and specific names. Species from south-eastern Australia were reviewed by Smith & Kershaw (1979) and various specific and generic groups from Victoria, Tasmania, Western Australia and North Queensland have been revised by Smith (1970, 1979, 1987), Smith & Kershaw (1972) and Kendrick, Sedgwick & Smith (1971).

Many of the external features are morphological adaptations characteristic of carnivores. The thin shell, composed mainly of conchin, is light and flexible, possibly an advantage when overcoming and ingesting large prey. Most species have a greatly elongated 'head' region and a wide fleshy foot; the shell is carried almost over the tail. The long 'head' contains a large, cylindrical buccal mass (Fig. 17.8B). Some species show a conspicuous, contrastingly coloured, longitudinal stripe along the mid-dorsal line of the head and body; its function is not known. Several species secrete very viscous, pigmented mucus which may help to immobilise the prey. Many have been recorded as active predators that attack and kill other snails and earthworms (Smith 1971, 1979b, 1980).

Jaws are absent and the radula consists of long, recurved, lanceolate teeth which often grade in size from small central teeth to large teeth towards the lateral margins of the radula (Fig. 17.51G–I; Smith 1987). This arrangement permits the mollusc to pulled whole large prey into the buccal cavity. The short digestive system is appropriate for a diet high in animal protein. Protuberances additional to the optic and sensory tentacles are present around the head of some species, and these may be sensory.

The reproductive tracts of several Australian and New Zealand species have been described (Smith 1970, 1979b; Climo 1977). The system is simple, usually with a large penis (Fig. 17.51E, F) with various specific internal microsculptures. Eggs of several species have been observed and are large, spherical to oval with calcareous, hard white shells, like small bird eggs (Powell 1949). The breeding cycle of one species has been documented by McLauchlan (1951). Ovoviviparity has been described in species of *Ouagapia* from islands in the Pacific by Kondo (1943), but it has not been observed in Australian taxa. It appears that breeding occurs when food and/or moisture are optimal as it has been observed in spring in some south-eastern Australian species (Smith 1970) and at the commencement of the wet season in some North Queensland taxa (Smith 1979b).

17. PULMONATA

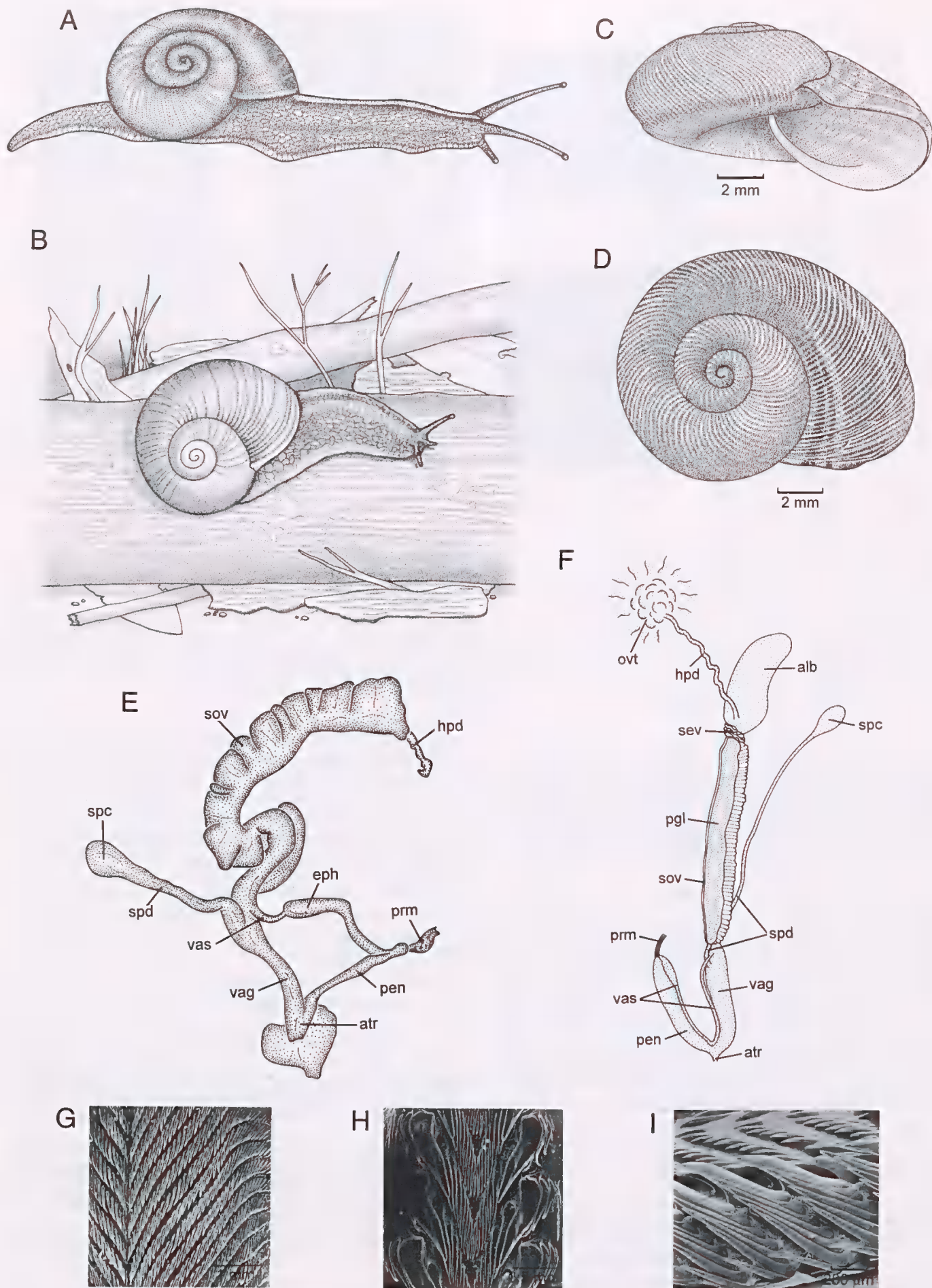


Figure 17.51 Family Rhytididae. A large family of carnivorous land snails. **A, B**, whole animals: **A**, *Strangesta* sp.; **B**, *Victaphanta atramentaria*. **C, D**, *Tasmaphena sinclairi*, shell: **C**, apertural view; **D**, apical view. **E, F**, reproductive tracts: **E**, *Austrorhytida capillacea*; **F**, *Victaphanta atramentaria*. **G–I**, portions of radulae: **G**, *Victaphanta* sp.; **H**, *Austrorhytida* sp.; **I**, *Strangesta* sp., showing articulation of the base-plates of the major tooth with those in adjacent rows. **alb**, albumen gland; **atr**, atrium; **eph**, epiphallus; **hpd**, hermaphrodite duct; **ovt**, ovotestis; **pen**, penis; **pgl**, prostate gland; **prrm**, penial retractor muscle; **sov**, spermoviduct; **spc**, spermatheca; **spd**, spermathecal duct; **vag**, vagina; **vas**, vas deferens. (**A, B**, after photographs by B.J. Smith; **E**, after Smith 1987; **F**, after Smith 1970) [**A–F**, C. Eadie; **G–I**, B.J. Smith]

Most species are confined to wet forest areas; rhytidids do not produce epiphragms and have a poor ability to withstand desiccation. The family ranges along the eastern Great Dividing Range from North Queensland and its offshore islands to Victoria, and south-eastern South Australia, Tasmania and the forests of south-western Australia. Several species are found in drier areas, and one species is found in open coastal heathland just south of Adelaide.

A number of species are thought to be preyed upon by bush-rats and blue-tongue lizards, as shells are found showing extensive damage. In the Sydney area, *Austrorhytida capillacea* preys on the introduced snail *Helix aspersa* where these species live sympatrically. This has been suggested in popular gardening magazines as a possible biological control agent for the helicid pest, triggering misguided suggestions of transplanting other rhytidids from rainforest to suburban gardens in other areas to control the introduced pest species.

The genus *Victaphanta* of south-eastern Australia shows affinity with the New Zealand *Paryphanta* and *Powelliphanta* in characters of the radula, reproductive system and shell. Tasmania and southern Victoria support the greatest diversity with 12 species in six genera. *Austrorhytida* (Smith 1987) also shows close affinities with the New Zealand *Rhytida*.

Superfamily ACAVOIDEA

Acavoideans are medium-sized to very large snails with shells that vary from globose to fusiform and discoidal. The shells are dextral, usually without prominent sculpture and apertural lamellae. The lip is either sharp or thickened and strongly reflected. The colour of the shell and animal is variable between species and some are brightly coloured. The radula consists of numerous unicuspidate teeth arranged in transverse rows. The central teeth are smaller than the lateral and marginal teeth (Kershaw 1989). The kidney is subtriangular without a ureter or links with a primary ureter that follows the kidney edge to a ureteric pore situated at the rear of the pallial cavity. The reproductive system is simple and the penis usually has an epiphallus. Acavoideans are oviparous or ovoviviparous and hermaphroditic.

Two families are recognised: the Acavidae, distributed in Madagascar, the Seychelles and Sri Lanka; and the Caryodidae, in eastern Australia. Acavoideans have been found in Pleistocene sediments of Madagascar (Zilch 1959) and Eocene deposits of eastern Queensland (Stanisic 1994a).

Family Caryodidae

Caryodids are medium-sized to large (15–100 mm in shell length) terrestrial snails (Pl. 32.4). The shell varies in shape from high-spired to conic to discoid. Usually the shell is banded or has a colour pattern; some have a distinctive sculpture. This endemic family contains Australia's largest terrestrial snail, *Hedleyella falconeri*, which attains a shell length of 80 mm. These large, conspicuous shells were collected by some of the earliest explorers and taken back to Europe for description. In his basic list of Australian land shells, Iredale (1937b) included all the species of the family, dividing them into four families because of the large variation in shell shape between the genera. Burch (1976b), Boss (1982) and Tillier (1989) placed the Australian species in a subfamily of the family Acavidae known from Madagascar and Sri Lanka. Solem (1978a) treated the family as a separate entity, placing it in the Acavoidea. Smith (1992) listed 13 species in seven genera.

Shell form varies a greatly between genera. *Caryodes* (Fig. 17.52A), *Brazierista*, *Pygmipanda* and *Pandofella* are bulimuliform (i.e. resembling the shape of bulimulid shells, in particular having a large, inflated last whorl), and in *Pandofella* the shell is reduced to a few whorls with a large open aperture (Pl. 32.4). Shells of *Hedleyella* species are subglobose (Fig. 17.52B); *Anoglypta*

(Fig. 17.52C), broadly conic with strong sculpture; and *Pedinogyra* species, large and discoidal (Fig. 17.52D). Smith (1992) listed seven valid genera and 15 valid species and subspecies in the family. In most species, the body is large and capable of considerable extension. Many of the shells and animals are strikingly coloured and patterned. The simple, unicuspidate radula teeth are strong (Fig. 17.52G, H). The animals are generally believed to feed on decaying vegetable and animal matter, but in captivity will also eat green plant material. The kidney is triangular and the narrow primary ureter opens at the base to a partially enclosed secondary ureter. Davies (1914) described the anatomy of *Caryodes dufresnii* from southern Tasmania, and in describing the pallial and alimentary organs, noted the large blood vessels and the large curved stomach.

Caryodids are oviparous hermaphrodites and have long been known for the large size of their eggs, sometimes compared with those of a small bird (Pilsbry 1894). The reproductive system has no accessory dart sac and the penis has no epiphallus in *Caryodes* and *Anoglypta* (Fig. 17.52E, F; Kershaw 1988a, 1988b). A short epiphallic swelling of the vas deferens occurs in *Pygmipanda* and *Hedleyella*, pressed tightly against the penis (Pilsbry 1894). There is no flagellum but a diverticulum enters the vagina adjacent to the bursal duct and free oviduct pores. The diverticulum of *Anoglypta* is reversed compared to the other genera. Sperm are transferred within mucous strings which can be seen throughout the terminal genitalia including the diverticulum (Kershaw 1988a). *Caryodes* species lay eggs in the spring in clutches of two to seven, in small depressions in the ground or in litter; hatching may take several weeks (Kershaw & Dartnall 1972, 1975). The life cycle is unknown, but individuals may not reach sexual maturity in the first year. Dartnall & Dartnall (1972) recorded chromosome numbers for several species. These range from $2n = 52$ in *Anoglypta* through $2n = 54$ in *Caryodes* to $2n = 58$ in *Pygmipanda*, *Pedinogyra* and *Hedleyella*.

Caryodids live in woodland to dry sclerophyll to rainforest habitats. Some species are confined to rainforest and all are threatened by forestry activities. The major predators are birds and small mammals. Shells broken in specific ways are found around anvil stones and in mammal runs. Bishop (1981) described predation in some Queensland species. Feeding activity is almost entirely nocturnal. The animal is dormant during the day and aestivates during dry periods, the aperture sealed with a thin epiphragm. Caryodids are generally found under logs or in moist litter, although some species will climb a short distance from the ground during rainfall. Bishop (1981) reported that *Hedleyella* hides in the strangler fig during the day and feeds on litter at night.

The family is endemic to eastern Australia and has a distribution from Queensland to Tasmania, largely along the Great Dividing Range on the mainland. *Caryodes* occurs in a wide range of habitats in Tasmania. The closest relatives of the Caryodidae appear to be the Acavidae of Sri Lanka, the Seychelles and Madagascar. Solem (1979a) listed a Pleistocene age for the Madagascan acavids but their Australian fossil history is very uncertain. Bruggen's (1980) suggestion that these snails have a Gondwanan origin is accepted by many workers. Stanisic (1994a) described *Praecaryodes antiquata* from Eocene deposits of mid-eastern Queensland.

A number of the species are rare and very localised; *Anoglypta launcestonensis* is considered one of the more rare and endangered land snails of the Australian fauna (Wells, Pyle & Collins 1983).

Superfamily BULIMULOIDEA

Bulimuloidean snails are terrestrial and have variable shells, ranging in shape from large bulimuloid and ovate-, or elongate-conic to depressed helicoid, turreted or cylindrical, rarely discoidal or further reduced. The aperture varies from large to small and in many taxa has one to numerous apertural lamellae and denticles. The sculpture is smooth or consists of weak to strong radial ridges sometimes crossed by spiral grooves. Shell

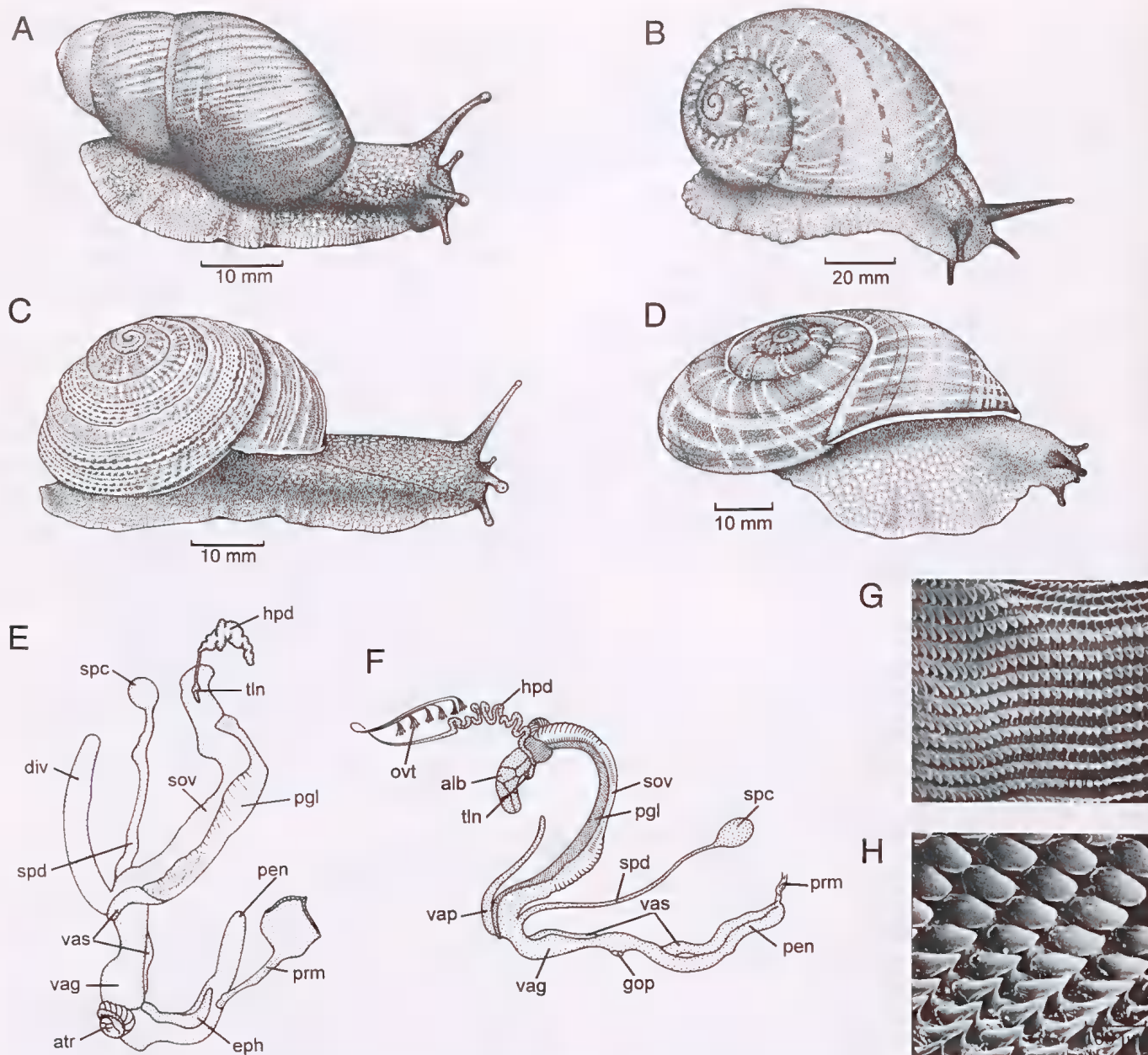


Figure 17.52 Family Caryodidae. A–D, animals: A, *Caryodes dufresnii*; B, *Hedleyella falconeri*; C, *Angolypia launcestonensis*; D, *Pedinogyra* sp. E, F, reproductive tracts: E, *Caryodes dufresnii*; F, *Pedinogyra hayii*. G, H, portions of radulae showing the simple, monocuspitate teeth: G, *Caryodes dufresnii*; H, *Pedinogyra* sp. alb, albumen gland; atr, atrium; div, diverticulum of spermathecal duct; eph, epiphallus; gop, gonopore; hpd, hermaphrodite duct; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; sov, spermoviduct; spc, spermatheca; spd, spermathecal duct; tln, talon; vag, vagina; vap, vaginal papilla; vas, vas deferens. (A, C, after photographs by R.C. Kershaw; B, D, after photographs by Australian Museum; E, after Kershaw 1988b; F, after Hedley 1889a)

[A–F, C. Eadie; G, H, B.J. Smith]

colour ranges from drab monochrome to a combination of brightly coloured bands and suffusions. The central tooth of the radula is typically as wide as the lateral teeth, and is usually unicuspidate; the laterals and marginals are variable. The cusps may be quite large in relation to the tooth shaft. A jaw is present (Pilsbry 1901, 1902, 1904).

The foot is holopodous. The kidney is triangular with or without a complete secondary ureter. The reproductive organs are simple. The penis may or may not have an epiphallus. In some bulimulids an epiphallic flagellum is present (Solem 1959a). Bulimuloideans are hermaphroditic, and oviparous or ovoviviparous.

Two families are included. The Urocoptidae are a speciose group of small snails from the southern United States, Central America and the West Indies. The Bulimulidae have a much wider distribution; the family is primarily South American, but also occurs in the West Indies, southern United States, New Zealand, Melanesia and Australia. Urocoptids are known from the Cretaceous of North America. The oldest known bulimulids are from the Eocene of South America (Parodiz 1969).

Family Bulimulidae

Bulimulids are ground-dwelling or arboreal terrestrial land snails (Pl. 31.2), typically with an ovate to cylindrical shell, that is highly variable in colour, sculpture, thickness, and size (Fig. 17.53A–D). Taxa from wetter areas have an elongate foot and neck, and are variable in colour, whereas the foot and neck of those from drier regions are extremely short and usually are light in colour. The classic world monographs by Pilsbry (1895–1896, 1897–1898, 1899, 1900b, 1902) were supplemented by the studies of Breure (1978, 1979), Breure & Eskens (1981), and Breure & Schouten (1985). Papers dealing specifically with the Australian species, which are grouped into the broadly defined genus, *Bothriembryon*, are the monograph of Western Australian species by Iredale (1939), notes on some Western Australian species by Kendrick & Wilson (1975), the review of the Tasmanian isolate, *Bothriembryon tasmanicus*, by Kershaw (1981a), and anatomical notes on Tasmanian, South Australian, and some Western Australian species by Breure (1978) and Kershaw (1986) (Fig. 17.53G, H). There maybe about 50 Australian species, most of which have relatively small ranges. Smith (1992) listed 32 species in two genera, including a single species of *Placostylus* (Fig. 17.23) from Lord Howe Island.

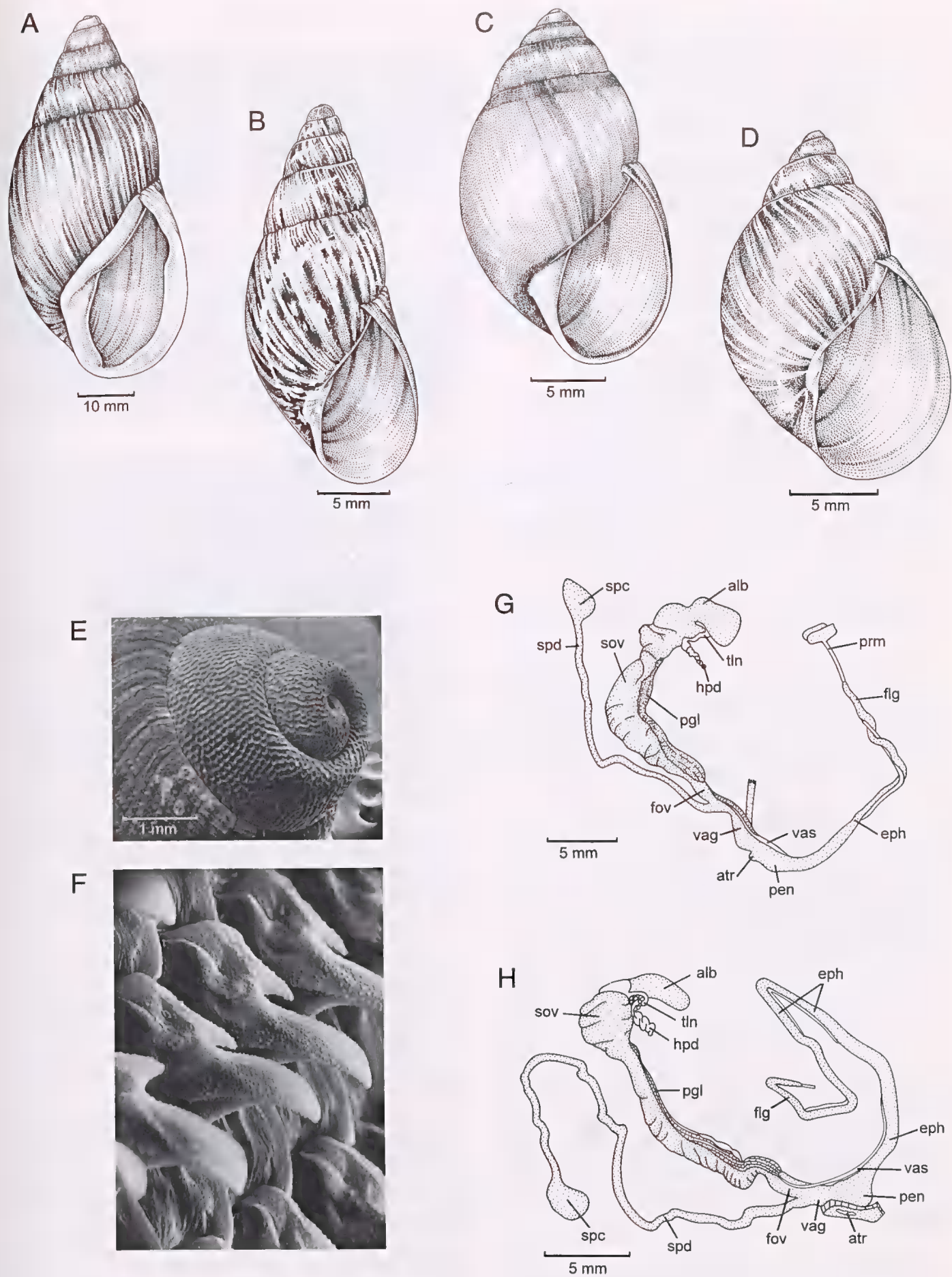


Figure 17.53 Family Bulimulidae. A–D, shells, apertural view: A, *Placostylus bivaricosus*; B, *Bothriembryon kingii*; C, *Bothriembryon melo*; D, *Bothriembryon tasmanicus*. E, *Bothriembryon bulla*, sculpture on shell apex and early spire. F, *Bothriembryon tasmanicus*, portion of radula showing lateral teeth (scale unknown). G, H, reproductive tracts: G, *Bothriembryon mastersi*; H, *Bothriembryon melo*. alb, albumen gland; atr, atrium; eph, epiphallus; flg, flagellum; fov, free oviduct; hpd, hermaphrodite duct; pen, penis; pgl, prostate gland; prrm, penial retractor muscle; sov, spermoviduct; spc, spermatheca; spd, spermathecal duct; tln, talon; vag, vagina; vas, vas deferens. (G, H, after Kershaw 1986)

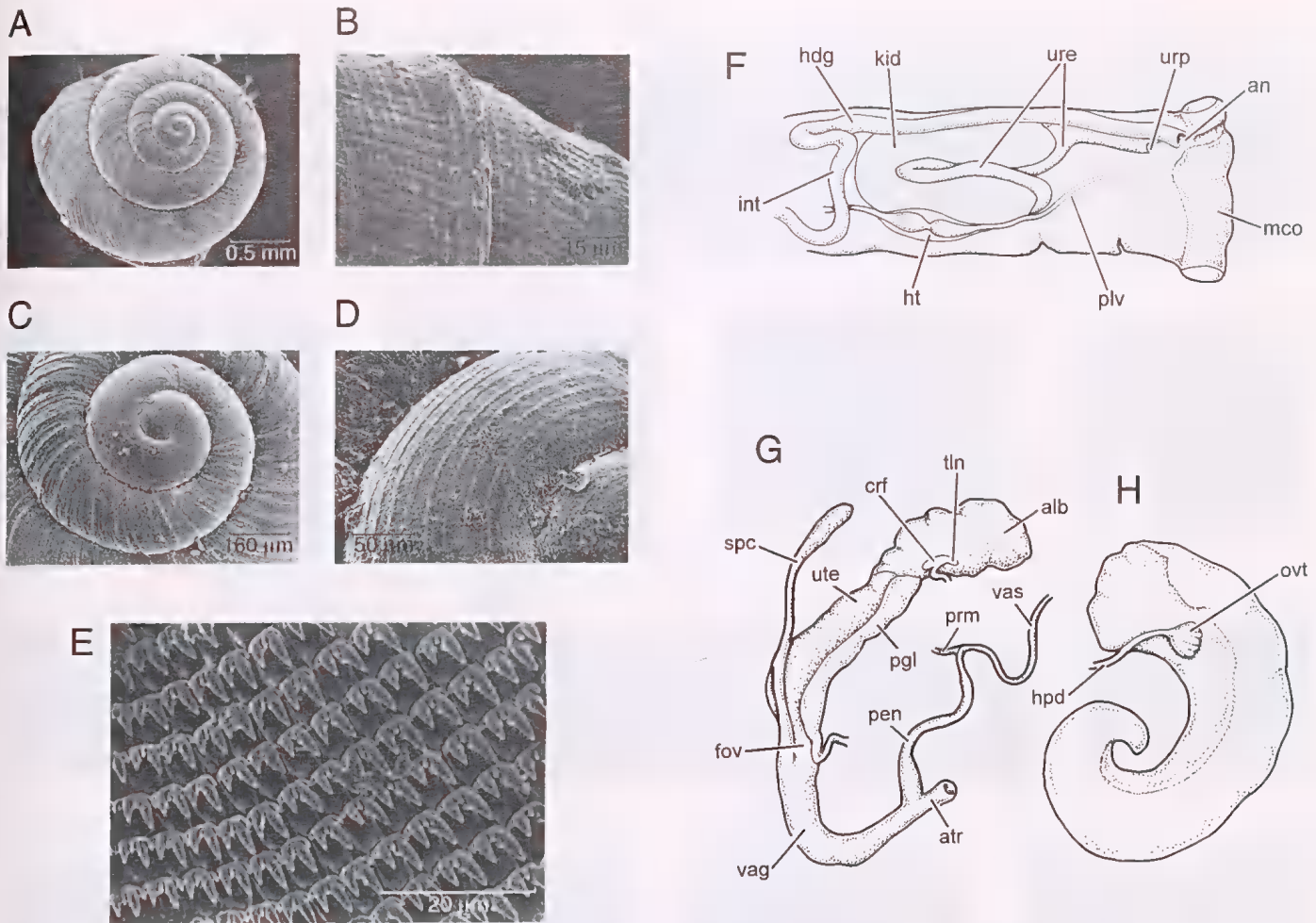


Figure 17.54 Family Punctidae. A–E, *Paralaoma caputspinulae*: A, shell, apical view; B, adult shell sculpture; C, spire of shell; D, details of protoconch sculpture; E, central region of radula. F–H, *Paralaoma aprica*: F, pallial complex; G, postapical section of reproductive system; H, apical portion of reproductive system. alb, albumen gland; an, anus; atr, atrium; crf, carrefour; fov, free oviduct; hdg, hindgut; hpd, hermaphrodite duct; ht, heart; int, intestine; kid, kidney; mco, mantle collar; ovt, ovotestis; pen, penis; pgl, prostate gland; plv, pulmonary vein; prm, penial retractor muscle; spc, spermatheca; tln, talon; ure, ureter; urp, ureteric pore; ute, uterus; vag, vagina; vas, vas deferens. (F–H, after Solem 1983)

status of several Australian punctid genera, and Solem (1983a) presented the first anatomical details of Australian species. Solem (1988b) provided distribution data on a species from central Australia. F.M. Climo (personal communication) has indicated that there are many undescribed taxa in Australia.

Australian species are small to minute (1–3 mm shell diameter) and conic to turbanate in shape (Fig. 17.54A), the shells usually dextral, rarely sinistral. The radula of punctids (Fig. 17.54E) is a diagnostic feature which separates them from charopids. The central tooth is small and tricuspidate. The latero-marginal teeth are bicuspidate with three minute accessory cusps and squarish basal plates, and the outer teeth have major cusps that become reduced without tendency to split into minor cusps. The jaw usually consists of separated vertical plates (Solem 1983a).

The punctid pallial complex has a sigmurethous ureter with a bilobed kidney, the lobes of which are almost equal (Fig. 17.54F). The lung roof shows little noticeable secondary venation.

The ovotestis consists of two teardrop-shaped lobes (Fig. 17.54H), and the terminal genitalia are typically long and slender (Fig. 17.54G). The epiphallus is penis-derived but weakly differentiated, and the penis usually has a vergic papilla. The female genitalia are also slender and the vagina has a smooth internal pilaster pattern.

Nothing is known of the life history or reproductive habits of the Australian species. They are usually found in drier fringe zones bordering the east coast moist forests and a few species extend into drier western areas including central Australia. The greatest diversity appears to occur in the south-east of the continent.

Punctids occur in the Northern Hemisphere, Africa, Australia, New Zealand, Subantarctic islands and some Pacific islands. Relationships of the Australian species to the Northern Hemisphere Punctidae are unknown. However, Solem (1983a) assigned a Pacific Basin species to the Holarctic genus *Punctum* rather than to the Australian-New Zealand *Paralaoma*, thus implying that there could be a major difference between these two geographical units.

Solem (1983a) estimated that 159 species level taxa are currently included in this family.

Family Charopidae

Charopids are terrestrial or semiarboreal land snails with a minute to small shell (1–7 mm shell diameter). The whorl count and shell shape are highly variable (Fig. 17.55A–I) and the umbilicus is closed to widely open. Shell sculpture is complex and the protoconch sculpture is diverse (Fig. 17.55J–N). Teleoconch sculpture typically consists of radial ribs with microsculpture of radial riblets and fine spiral cords (Fig. 17.55O–R). Occasionally the sculpture may be modified, reduced or lost. Apertural barriers are present in several lineages and the lip is simple. Shell colour pattern varies from uniform to tessellated.

The Charopidae are one of the largest families of land snails in Australia with over 300 described and undescribed species (J. Stanisc personal communication). Studies of the Australian species have been largely 'shell-based' and almost exclusively confined to listings in faunal checklists. Hedley (1924), Solem (1984a), Smith & Kershaw (1985) and Stanisc (1987, 1990) dealt specifically with Australian charopids. With the exception of

17. PULMONATA

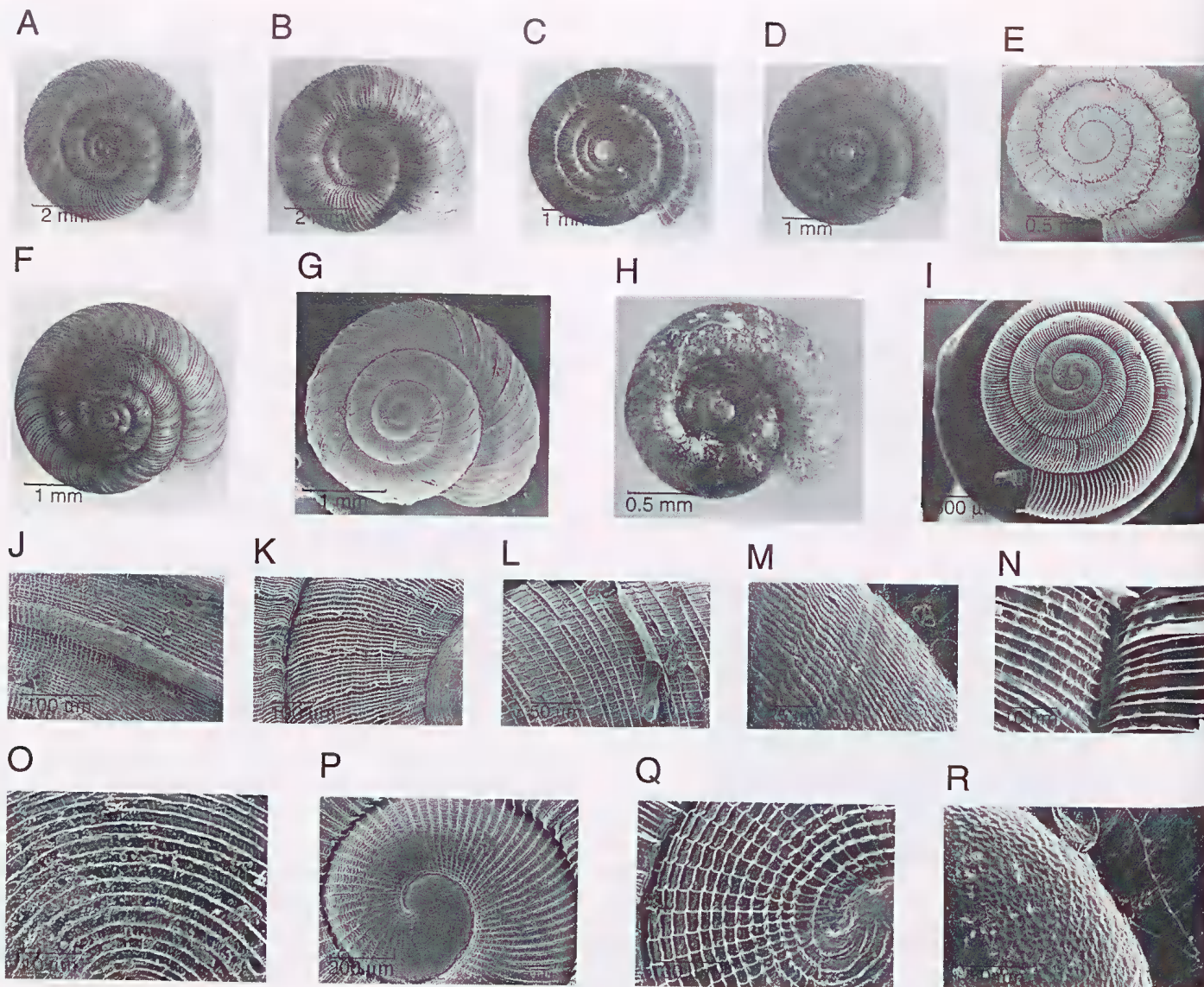


Figure 17.55 Family Charopidae. A–I shells: A, *Gyrocochlea curtisiana*; B, *Nautiliropa omicron*; C, *Rhopodon kempseyensis*; D, *Setomedeia janae*; E, *Egilomen cochlidium*; F, *Ngairea canaliculata*; G, *Coenocharopa macromphala*; H, *Letomola contortus*; I, *Rotacharopa densilamellata*. J–N, postnuclear sculpture: J, *Biomphalopa recava*; K, *Setomedeia monteithi*; L, *Coenocharopa multiradiata*; M, *Lenwebbia protoscrobiculata*; N, *Rotacharopa annabelli*. O–R, nuclear sculpture: O, an undescribed charopid species; P, *Elsothera nautilodea*; Q, *Rotacharopa annabelli*; R, *Lenwebbia protoscrobiculata*. [Queensland Museum]

Hedley (1889a), who illustrated the jaw of *Hedleyoconcha delta*, and Odhner (1917), who figured the jaw and radula of *Pilsbrycharopa tumidus*, malacologists of the late 19th and early 20th Century concentrated on shell features for determining species and constructing generic frameworks. Literature references to Australian charopid species are scattered, but Iredale (1937a) provided a useful compilation of earlier records. Iredale (1937c, 1939, 1941) introduced a number of new genera and species and Solem (1984a) reviewed a number of Northern Australian species. Solem's (1983a) revision of the Pacific Island species provided significant basic data on the family, including several Australian species, as did Climo (1969, 1970, 1978) for New Zealand species. Anatomical details were given by Smith & Kershaw (1985) and Stanisc (1987, 1993b, 1993c) for several genera and species from the Tasmania–Victoria and northern Queensland areas respectively. Solem (1988b) provided further distributional data on northern and central Australian species. Stanisc (1990) reviewed 50 species of Australian Charopidae and provided comprehensive anatomical and distributional data. However, knowledge of this numerically large family of land snails is still rudimentary. Smith (1992) listed 156 species, including 29 from Lord Howe Island and Norfolk Island.

Most charopid animals are generally light in colour with dark eyespots. In semi-arboreal species the ommatophores, neck region and sides of the foot may be pigmented. A weak caudal horn may be developed, especially in arboreal taxa. The tricuspidate central tooth in the radula (Fig. 17.56A–D) is slightly to distinctly smaller

than the lateral teeth. The laterals and marginals are tricuspidate and multicuspidate (Solem 1983a; Smith & Kershaw 1985; Stanisc 1987, 1990). The separate square plates that form the jaw may be fused in larger species. Modifications to the basic radular pattern occur in more specialised arboreal taxa (Stanisc 1990).

Charopids have fused pallial gonoducts in which the prostate is a lateral outpocket of the uterine chambers. The ovotestis may consist of one or two (or more in taxa with secondary shell modifications) clumps of alveolar follicles embedded in the upper parts of the digestive gland. The genitalia are generally short and stout. The epiphallus is derived from the vas deferens and is usually well developed (Fig. 17.56G). Accessory appendages may be present (Smith & Kershaw 1985; Stanisc 1987, 1993b). The penis may have a verge and simple or complex pilasters (Fig. 17.56H); a penis sheath may or may not be present. The female genital system has a vagina with prominent pilasters and a spermatheca with expanded base, narrow stalk and subcircular head that lies at the base of the albumen gland. Spermatophores (Fig. 17.56I) are used in sperm transfer (Stanisc 1990).

The charopid pallial complex has a complete or incomplete (Stanisc 1987, 1990, 1993b, 1993c) sigmurethrous ureter (Fig. 17.56E, F). The kidney is generally bilobed with the lobes either equal or unequal in length. Solem (1983a) showed that the rectal lobe is longer in most Pacific island species. In contrast, the pericardial lobe is longer in a large number of Australian species (Stanisc 1987, 1990).

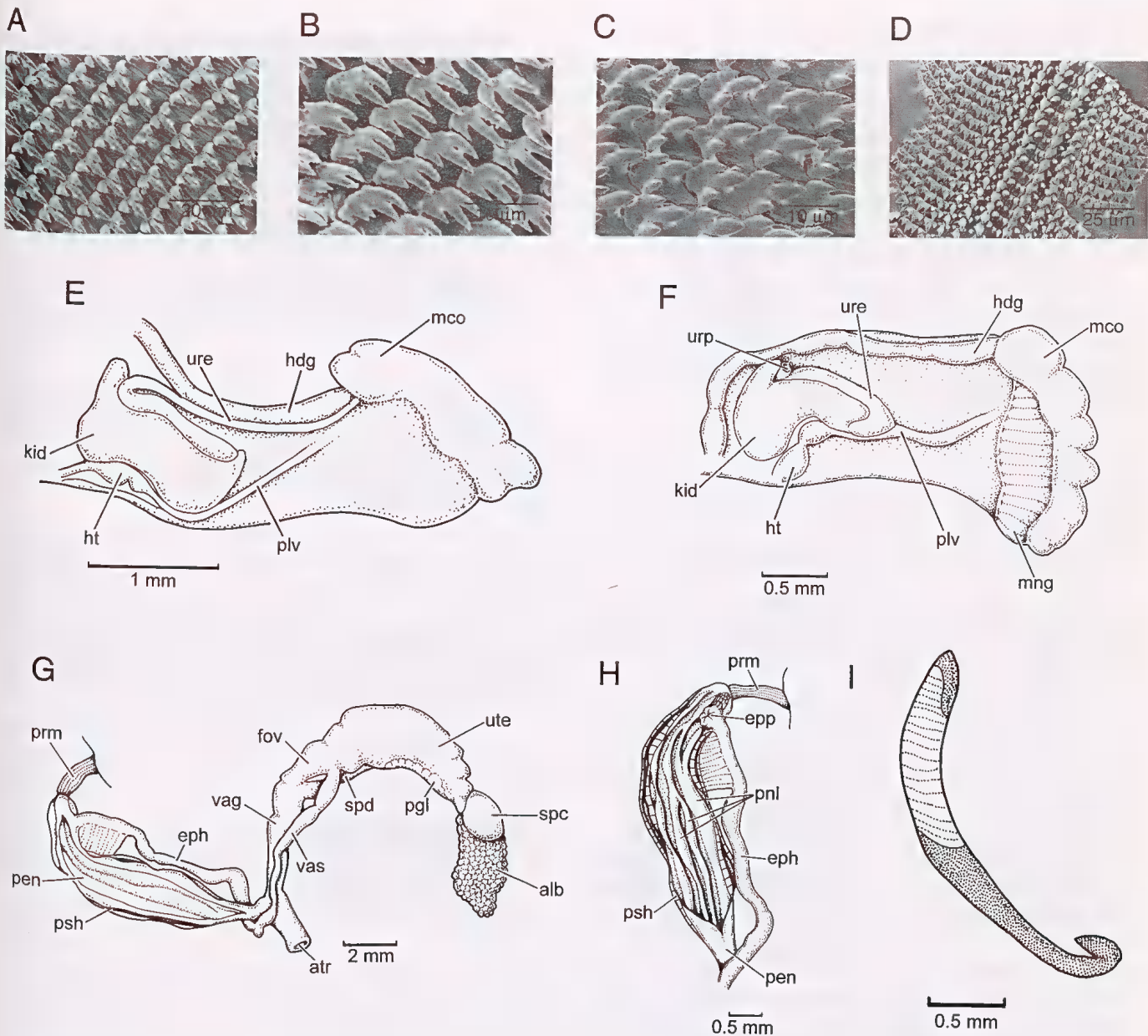


Figure 17.56 Family Charopidae. A–D, portions of radulae: A, B, *Biomphalopa recava*, central region (A), marginal teeth (B); C, *Hedleyoconcha delta*, central and lateral teeth showing anterior flare; D, *Letomola contortus*, transverse rows of teeth showing the reduced central tooth, enlarged tricuspid lateral teeth and serrate marginal teeth. E, F, pallial regions: E, *Gyrocochlea paucilamellata*; F, *Mussonula fallax*. G–I, *Gyrocochlea paucilamellata*, reproductive anatomy: G, reproductive system; H, details of penis interior; I, spermatophore. alb, albumen gland; atr, atrium; eph, epiphallus; epp, epiphallic pore; fov, free oviduct; hdg, hindgut; ht, heart; kid, kidney; mco, mantle collar; mng, mantle gland; pen, penis; pgl, prostate gland; plv, pulmonary vein; pnl, penial pilasters; prrm, penial retractor muscle; psh, penis sheath; spc, spermatheca; spd, spermathecal duct; ure, ureter; urp, ureteric pore; ute, uterus; vag, vagina; vas, vas deferens. (E–I, after Stanisc 1990)

[A–D, Queensland Museum; E–I, B. Scott]

Australian charopids were the focus of early attention by such workers as Legrand (1871), Petterd (1879a) and Hedley (1924), but still very little is known about their habits and life histories. They are generally categorised as litter dwellers. However, individuals have been collected from under logs and rocks, among moss, under bark of trees and even from the axils of palm trees (Stanisc 1987, 1990). In eastern Australia, the Charopidae appear to be closely associated with rainforests. Very few species have made the transition to adjacent drier sclerophyll forests.

The Charopidae have a Gondwanan distribution (Bruggen 1980). As well as Australia (including Lord Howe Island and Norfolk Island), they occur in South America, southern North America, southern Africa, New Zealand, Juan Fernandez Island, St Helena Island, islands of the Pacific, Subantarctic islands, Indonesia, the Philippines and Papua New Guinea. Historically, the south-eastern region has been considered the centre of diversity of the family in Australia. However, the findings of rainforest surveys (Burch 1976c) and the comments of Stanisc (1987, 1990, 1993b, 1993c, 1994b) indicate that significant radiations of Charopidae are

represented in the subtropical and tropical rainforests of eastern Australia. Additionally, Solem (1983a) mentioned a large, undescribed fauna in south-western Australia.

Stanisc (1990) suggested that the Australian charopids have more in common with New Zealand rather than with Pacific island taxa. Solem (1984a) showed that some species, such as *Discocharopa aperta*, have extensive ranges, including the Philippines, Indonesia, northern Australia, Kermadecs, Fiji and Society Islands, and some, for example, *Pilsbrycharopa tumidus*, have at least conchological affinity with Indonesian-New Guinean taxa. In contrast, Stanisc (1987) showed that *Oreokera cumulus* and *O. nimbus* have geographically and altitudinally restricted ranges in the higher mountains of northern Queensland. Two subfamilies, Charopinae and Rotadiscinae, are present in Australia (Stanisc 1990).

Charopids have no known fossil record in Australia though Ladd (1958) recorded species from Miocene and Pleistocene deposits of some Pacific islands.

Family Helicodiscidae

Helicodiscids are minute, terrestrial snails with a nearly flat spire, a low whorl count and very wide umbilicus, prominent spiral ridges, complex apertural barriers, and usually a very strongly reflected and thickened lip. Live specimens of the one Australian species, *Stenopylis coarctata*, have been taken from the undersides of small rocks on flood plains and from limestone talus. The animal is orange-yellow with black eye spots. Only a single young is brooded at a time. The radula has normal central and lateral teeth, but the marginals are greatly modified (Solem 1984a).

Stenopylis is easily separated from other minute Australian land snails by its minute size (1.4–1.8 mm shell diameter), about 3.5 whorls that do not increase in width, prominent spiral ridges, wide umbilicus, and its grossly expanded lip (Fig. 17.57). Members of the Charopidae and Punctidae have prominent radial shell sculpture and lack the expanded lip.

The typical North American genera, *Helicodiscus*, *Hebetodiscus* and *Pseudiscus*, have been reviewed by Pilsbry (1948). A somewhat modified, monotypic genus, *Polygyriscus*, from near Radford, Virginia, was referred to the Helicodiscidae by Solem (1975), who also summarised the monotypic genus, *Stenopylis* (Solem 1984a). Less than twelve extant species are known.

No data are available on the diet of *Stenopylis*. The modified marginal teeth contrast with the typical central and laterals (Solem 1984a). Whether this change indicates an altered diet or is a function of small size is unknown.

Some data on embryo size and their pattern of presence in June-collected material from central Australia were summarised, and a tentative hypothesis concerning the reproductive process was presented by Solem (1984a). The life span of *Stenopylis* is unknown; it is probably more than two years.

The few live collections have come from streamside habitats, although *Stenopylis* is very common throughout the Kimberley region of Western Australia, Northern Territory above the Roper River, and much of central Australia. Aestivating specimens have a thin, mucoid epiphragm.

The Helicodiscidae have a very unusual, disjunct range. Most genera are found in southern Canada and the United States, though some extralimital greenhouse records of *Helicodiscus* are known. The monotypic *Stenopylis* ranges from the Philippines and Indonesia to New Guinea, the Solomon Islands and most parts of

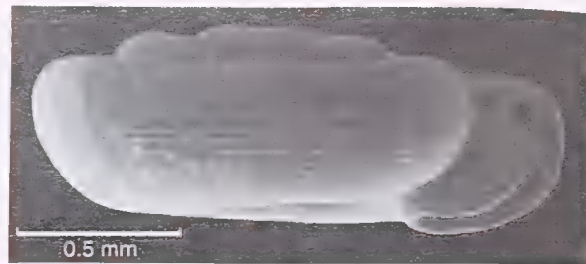


Figure 17.57 Family Helicodiscidae. Shell of *Stenopylis coarctata*, found in the hot dry areas of northern and central Australia; this is the only Australian helicodiscid species. [A. Solem]

the northern half of Australia; it is not present on the South-East Asian mainland. *Stenopylis coarctata* is of no known economic significance and has no known fossil record.

Family Arionidae

Arionids are terrestrial slugs native to northern Europe, North America and Asia. Several species have been introduced throughout the temperate world by recent human migration (Smith 1989). Museum specimens indicate that isolated specimens of the large *Arion ater* occurred in Sydney in the early 1900s, but not recently, and this species does not appear to be established in Australia. *Arion hortensis* was recorded from several parts of south-eastern Australia by Cotton (1954) and Smith & Kershaw (1979). Long (1970) recorded a third species, *Arion intermedius* (Fig. 17.58B) from Victoria; its recorded range was extended into New South Wales and Tasmania by Smith & Kershaw (1979, 1981).

Arionids are small to very large slugs (up to 150 mm in length) with prominent body tubercles. The shell is reduced to a few calcareous granules embedded in the posterior part of the mantle or entirely absent. The pneumostome is on the right anterior lateral margin of the mantle, a feature which separates arionids from the other common introduced slugs, the limacids and milacids, in which the pneumostome is situated towards the posterior margin (Fig. 17.58A). There is no dorsal keel, the foot is usually broader than the body with a prominent foot fringe and there is a prominent caudal gland. Body colour and pattern vary from species to species.

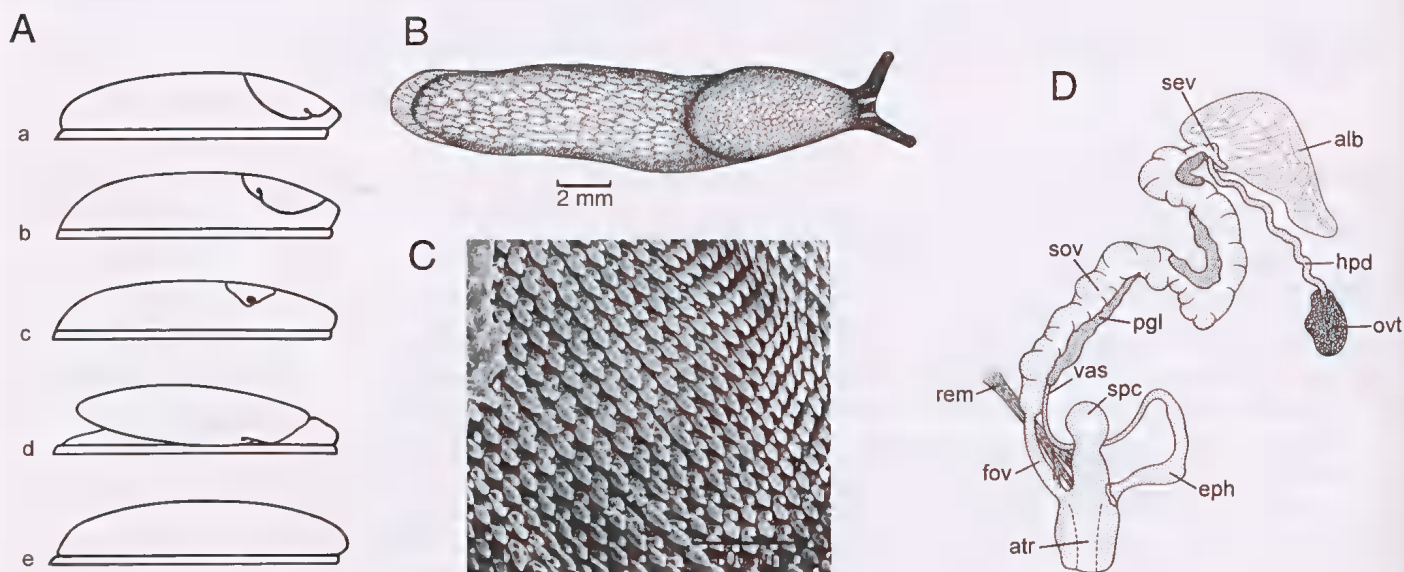


Figure 17.58 Family Arionidae. A, slug body forms in outline: a, Arionidae; b, Limacidae and Milacidae; c, Athoracophoridae; d, Cystopeltidae; e, Systellommatophora. B–D, *Arion intermedius*, an introduced slug from Europe, is common throughout south-eastern Australia; B, animal, dorsal view; C, portion of radula; D, reproductive tract. alb, albumen gland; atr, atrium; eph, epiphallus; fov, free oviduct; hpd, hermaphroditic duct; ovt, ovotestis; pgl, prostate gland; rem, retractor muscle; sev, seminal vesicle; sov, spermoviduct; spc, spermatheca; vas, vas deferens. (A, after Smith & Kershaw 1979; D, after Quick 1960)

[A, B, D, C. Eadie; C, B.J. Smith]

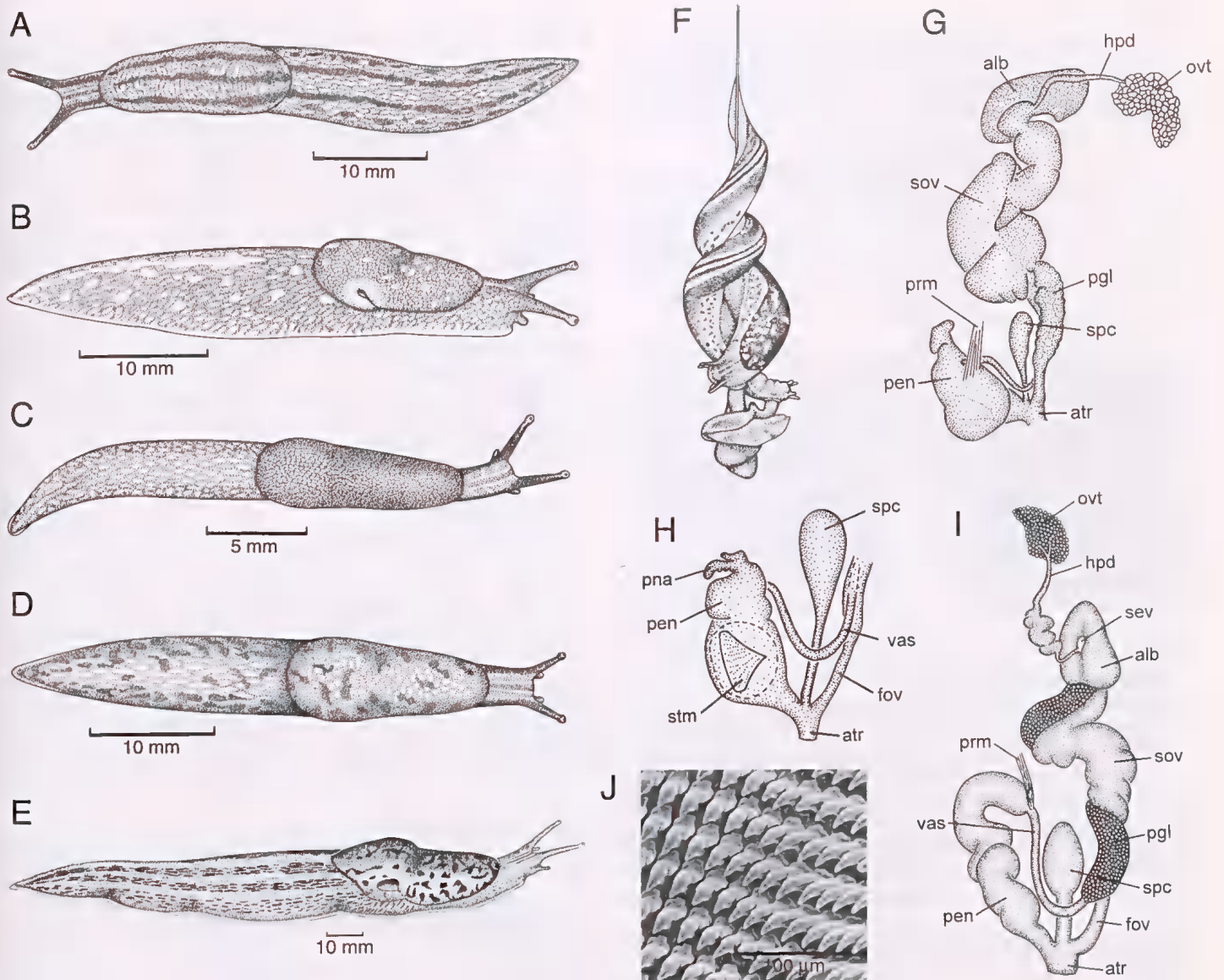


Figure 17.59 Family Limacidae. All limacid slugs in Australia are introduced, and are classed as pest species. A–E, animals: A, *Lehmannia nycetelia*; B, *Lehmannia flava*; C, *Deroceras panormitanum*; D, *Deroceras reticulatum*; E, *Limax maximus*. F, *Limax maximus*, a mating pair. G–I, reproductive systems: G, *Deroceras reticulatum*; H, *Deroceras reticulatum*, details of distal section of reproductive tract; I, *Lehmannia nycetelia*. J, *Lehmannia nycetelia*, portion of radula. alb, albumen gland; atr, atrium; fov, free oviduct; hpd, hermaphroditic duct; ovt, ovotestis; pen, penis; pgl, prostate gland; pna, penial appendix; prm, penial retractor muscle; sev, seminal vesicle; sov, spermooviduct; spc, spermatheca; stm, stimulator inside penis; vas, vas deferens. (A–E, drawn from live animals; F, after Burch 1976; G, modified after Quick 1960; H, modified after Kerney & Cameron 1979; I, after Quick 1960) [A–I, C. Eadie; J, B.J. Smith]

Most arionids are green plant feeders though *Arion intermedius* probably feeds mainly on fungi (Quick 1960). The anatomy of the three species recorded from Australia is given by Quick (1960). The jaw is ribbed and the radula consists of a tricuspidate central tooth, bicuspidate laterals; the short, wide marginals have long mesocones, and ectocones may or may not be present (Fig. 17.58C). The pericardium is enclosed by the kidney (Runham & Hunter 1970).

Members of this family are protandric hermaphrodites. The reproductive tracts of the three introduced species are described by Quick (1960); that of *Arion intermedius* is illustrated in Figure 17.58D. The sequence of maturation of the reproductive tract, and the histochemistry of the various secretions produced at different stages in the sequence, were described for *Arion ater* by Smith (1965, 1966a). Smith (1966b) also described the central nervous system of this species and recorded the presence of neurosecretory material. Arising from these studies, a possible neurosecretory control system of the maturation of the reproductive cycle was postulated (Smith 1967a). In some species mating occurs in spring and early summer and the young hatch in autumn. In others, mating occurs in late summer, and eggs laid in autumn overwinter to hatch in spring (Quick 1960). No detailed studies have been carried out on Australian populations.

In Australia *Arion ater* has only been found in gardens and other intensively cultivated areas and *Arion hortensis* has only been recorded from garden and pasture areas in cooler regions. *Arion intermedius* appears widespread and common in wet forest areas of south-eastern Australia, even in more remote areas such as the Franklin River of south-western Tasmania (Malcolm 1987).

One interesting behavioural pattern seen in many arionids is variation in extreme head-withdrawal behaviour which is species specific. On extreme withdrawal *Arion intermedius* contracts the main skin tubercles into pointed structures, giving rise to the common name of hedgehog slug. *Arion ater* takes up a slow body sway if agitation persists on extreme withdrawal (Quick 1960).

Although *Arion ater* and *Arion hortensis* are major pests in western Europe, their establishment is so tenuous in Australia that they have little or no economic significance.

Superfamily LIMACOIDEA

Limacoidean shells vary from very small to very large and from thin and fragile to thickened and solid. Shell shape is highly variable and in many taxa the shell is reduced to an ear-shaped dorsal plate or internal fragments; rarely it is completely absent. Sculpture usually consists of incised spiral grooves, with or

without radial costae. The shell is generally smooth and shiny, often colourful. Apertural lamellae are sometimes present. The radula has short, stubby teeth with elongate basal plates. The marginal teeth have one to many cusps with the outer elevated on the middle cusp (Solem 1974). There are usually many more teeth than in an arionoidean radula.

The sole of the foot is either undivided, or mostly tripartite in those forms with a reduced shell. The mantle is often extended as flaps of tissue that cover the shell. A caudal horn and fossa are usually present. In contrast to the Arionoidea, the reproductive system is complex and frequently has elaborate accessory appendages (Solem 1976). Limacoideans are hermaphroditic, and either oviparous or ovoviviparous.

The superfamily includes 12 families. Two have widespread distributions, including Australia, one is an Australian endemic and four have been introduced into Australia. Among five that are not represented in Australia, the Trigonochlamydidae are relatively small slugs from Central Asia; the monotypic family Aillyidae occurs in West Africa; the Urocyclidae include both shelled and slug-like forms in Africa; the Thyphorellidae are a monotypic family of slugs from São Tomé Island, in the Gulf of Guinea; and the Parmacellidae are basically a group of Palearctic slugs.

The family Helicarionidae, which Tillier (1989) placed near the more advanced helicoidean families, is large and diverse. Its several subfamilies range from the Holarctic into the Pacific Islands, Papua New Guinea, Malaysia and Asia. Australia (including Lord Howe Island and Norfolk Island) has a diverse helicarionid fauna (Smith 1992). A few representatives also occur in tropical America and eastern Africa. The Trochomorphidae occur through Polynesia and Micronesia with additional species in New Guinea, Indonesia, Malaysia, the Philippines, Japan, China and India; only one species occurs in Australia. The Cystopeltidae are a group of slugs restricted to south-eastern Australia where the family is represented by several species. Tillier (1989) considered that *Cystopelta* belongs to the Punctidae on the basis of general similarity in digestive tract morphology and the central nervous system.

Among the introduced groups, the Milacidae and Limacidae are Palearctic slugs, the Testacellidae are a group of unusual carnivorous semi-slugs from Western Europe, and the Zonitidae are basically shelled, Holarctic group with some representatives on the Hawaiian Islands.

The earliest record of the Limacoidea is from the Palaeocene of Europe (Zonitidae).

Family Limacidae

Limacids are medium to large terrestrial slugs, 25–200 mm in body length. The respiratory orifice is posterior to the middle of the right mantle margin (Figs 17.58A, 17.59B, E), and a keel present at the posterior end of the body does not reach the mantle (Fig. 17.59A–E). The family is native to Europe and North Africa, but several species are accomplished world travellers (Smith 1989). Limacids were first recorded from Australia by Quoy & Gaimard (1824) who described two species anew from Port Jackson. Musson (1890) reviewed the introduced slug fauna and recorded four limacid species from many parts of Australia. More recently, a comprehensive revision of limacids in Australia was published by Altena & Smith (1975) in which five species were recorded from many localities.

The narrow, streamlined body is enclosed in a thick muscular body wall with no separate visceral mass. The mantle shield is oval, covering the anterior portion of the body and bears concentric striations. The shell is internal and reduced to a small calcareous plate covered by the mantle. Colour and pattern are highly variable though some species have fairly constant, species-specific markings. Mucus colour and viscosity are also variable and are useful characters for identification (Altena & Smith 1975). The foot is aulacopodous, the sole is tripartite and

locomotion is rhythmic with direct waves over the middle field. Most limacids feed on green plants though some are omnivorous. The digestive tract is long and has a large crop. The jaw is smooth with a central protuberance and the radula has bicuspidate lateral teeth and narrow, bifid marginal teeth (Fig. 17.59J).

The reproductive anatomy of all the limacid species found in Australia has been described by Altena & Smith (1975) (Fig. 17.59G–I). All are protandric hermaphrodites and self-fertilisation is known for several species. The penis lacks an epiphallus and no spermatophores are produced (Quick 1960). Laying occurs in early spring; several clutches of small, colourless and almost translucent eggs are laid in damp soil under litter. Hatching occurs in about 10 days under favourable conditions of food and moisture. Maturation can be reached in about 10 weeks. A second generation can be produced in the same year if conditions are favourable. *Limax maximus* mates at the end of a long string of mucus hanging from a branch of a tree often several metres above the ground (Fig. 17.59F; Burch 1976a). After withdrawal, the animals reascend the string (Quick 1960).

Limacids are usually found in damp situations in habitats modified by introduced plants. In Australia several species are only found in fairly close proximity to human habitation, and some use their ability to get through extremely small spaces to enter houses and outbuildings for shelter. Very few birds will take them, probably because of the viscous mucus; ducks and some rodents prey on these slugs though they are not a major cause of mortality. Slugs are usually active at night in damp conditions and seek cool, moist shelter at other times, being very susceptible to desiccation. Some populations are infested with a minute white mite that lives on the body surface and feeds on the mucus produced as a general body secretion.

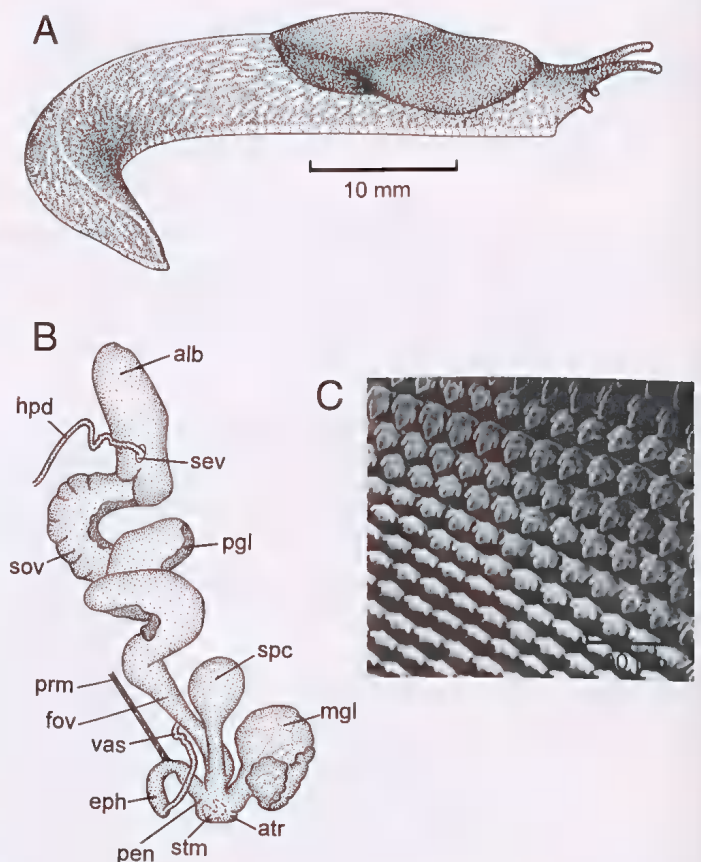


Figure 17.60 Family Milacidae. *Milax gagates*, an introduced slug, is the only milacid found in Australia. A, animal, lateral view, showing the keeled tail. B, reproductive tract. C, portion of radula. alb, albumen gland; atr, atrium; eph, epiphallus; fov, free oviduct; hpd, hermaphroditic duct; mgl, mucous gland; pen, penis; pgl, prostate gland; prm, penial retractor muscle; sev, seminal vesicle; sov, spermoviduct; spc, spermatheca; stm, stimulator inside penis; vas, vas deferens. (A, drawn from live animal collected in Victoria; B, after Pilsbry 1948) [A, B, C. Eadie; C, B.J. Smith]

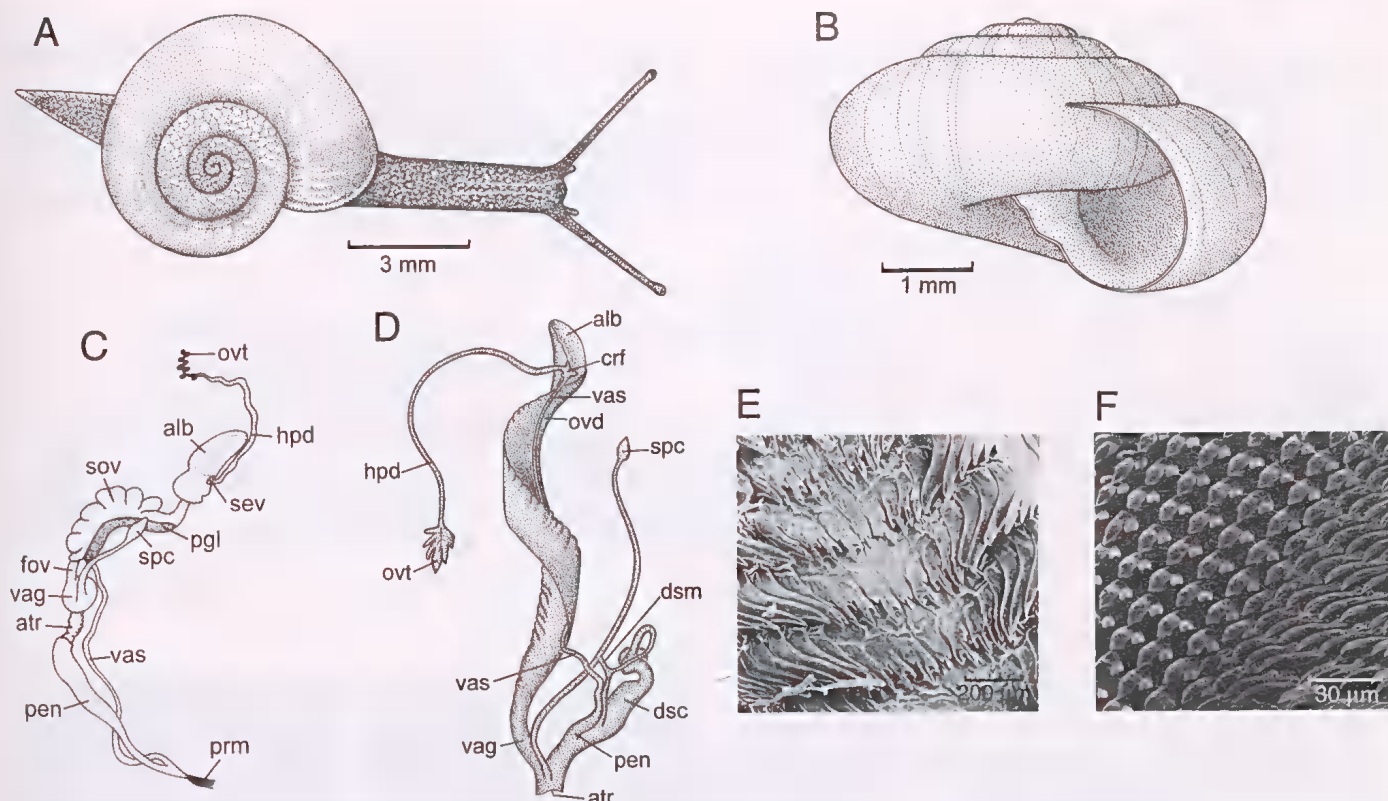


Figure 17.61 Family Zonitidae. A, *Oxychilius* sp., animal, dorsal view, showing the placement of the shell. B, *Zonitoides arboreus*, shell. C, D, reproductive tracts: C, *Oxychilius cellarius*; D, *Zonitoides arboreus*. E, F, portions of radulae: E, *Oxychilius draparnaldi*; F, *Zonitoides* sp. alb, albumen gland; atr, atrium; crf, carrefour; dsc, dart sac; dsm, dart sac retractor muscle; fov, free oviduct; hpd, hermaphroditic duct; ovd, oviduct; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; sev, seminal vesicle; sov, spermoviduct; spc, spermatheca; vag, vagina; vas, vas deferens. (A, from live specimen collected in eastern Victoria; C, after Rigby 1963; D, after Bartsch & Quick 1926) [A–D, C. Eadie, E, F, B.J. Smith]

Several species are of considerable economic significance as major pests of young plants. *Deroceras reticulatum*, in particular, is a serious pest of young pasture and cereal crop seedlings. Metaldehyde baits are used to combat its attack in the wheat-growing areas of southern Australia. This is particularly necessary where 'chemical ploughing' has been used, as stubble left in the field from the previous year's crop allows a winter and spring build-up of the slug populations. Details of the economic importance of limacid slugs, mainly in Europe and America, were given by Runham & Hunter (1970). Australian information on signs of infestation and methods of treatment are given in state agricultural advice pamphlets (for example, Comery & Ward 1985).

The family includes about 10 to 12 genera worldwide, mainly in the temperate and subtropical regions. Three of these occur in southern Australia – *Deroceras*, *Lehmannia* and *Limax*.

Family Milacidae

Milacids are medium-sized (40–70 mm body length) terrestrial slugs (Fig. 17.60A). Though the group has been treated as a subfamily of the Limacidae by several workers (Baker, H.B. 1956; Burch 1976b), it is here treated as a separate family, following Altena & Smith (1975). The family is native to Europe, but several species are accomplished world travellers (Smith 1989) and the Australian species was introduced by Europeans within the last 200 years. The first milacid from Australia was described by Quoy & Gaimard (1824) as a new species from Port Jackson. The same species was described as new three more times by Selenka (1865) and Tate (1881). Subsequently, Musson (1890) reviewed the introduced slug fauna of Australia and showed that there was only one species of milacid, *Milax gagates*, which had become extremely widespread across southern Australia. More recently a comprehensive revision of the milacid records in Australia was published by Altena & Smith (1975); it included anatomical details of the species.

The narrow, streamlined milacid body is enclosed in a thick, muscular body wall. The visceral mass is not separated. The mantle shield is oval and bears a horseshoe-shaped groove. The

internal shell is covered by the mantle. It is thicker than in the Limacidae and has a median, non-spiral nucleus near the posterior margin. The pneumostome is situated behind the middle of the right mantle margin and the dorsum has a pronounced medium keel that extends up to the posterior mantle margin (Fig. 17.60A). There are no colour bands on the body, the animal is a uniform black or brown. The foot is aulacopodous and the sole tripartite. The herbivorous *Milax gagates* has a long digestive tract with a forward-directed loop. The jaw is smooth and the radula has bicuspidate lateral teeth and narrow, bifid marginal teeth (Fig. 17.60C). The pedal gland lies free in the body cavity and the right optic tentacle is situated to the left of both penis and vagina.

The reproductive anatomy of *Milax gagates* was described by Altena & Smith (1975). It is a protandric hermaphrodite. Unlike limacids, it has a long epiphallus and a brown chitinous spermatophore is produced. Together the penis and vagina enter the atrium which contains a long, almost smooth stimulator (Fig. 17.60B). Laying occurs in spring and early summer and a second generation may be produced in autumn. The small, colourless eggs are almost translucent gelatinous spheres laid in damp soil in several clutches. Hatching can occur in about 10 days under favourable conditions.

Milax gagates is usually found in damp situations in habitats modified by human settlement or activity, such as suburban gardens, cleared land and main access routes into the bush areas. They congregate under logs in deep shelter in dry periods. They are active on cool damp nights when they feed on soft plant material; they can be major pests of young plants and fruit.

The three to six genera in this small family occur mainly in the temperate regions of the world (Quick 1960). Only one species, *Milax gagates*, is so far recorded from Australia but one or two other members of the family are known as world travellers and may be found in Australia in the future. Methods of population estimation and control of the species are detailed in Runham & Hunter (1970).

Family Zonitidae

Zonitids snails (Fig. 17.61A) are known as glass snails because the shell is usually thin, semi-transparent and featureless. These terrestrial snails are found mainly in Europe, northern Asia and North America but several species are widespread as introductions, chiefly in the temperate and subtropical regions of the world (Smith 1989).

Seven species are known to have been introduced into Australia from Europe or North America. The first two recorded were described by Cox (1864, 1868) as new species, but were later shown to be species introduced from Europe (Musson 1890) and America (Bishop 1978). Long (1972) revised the zonitids introduced into Victoria, adding two further species to the Australian list.

Zonitids in Australia have mainly small to medium-sized (up to 15 mm or greater in diameter), low-spined, thin, often semi-transparent shells, with little or no sculpture (Fig. 17.61A, B). The animal has a foot margin defined by a pedal groove which may form a caudal mucous gland. The jaw is smooth with a median projection and the radula usually has few teeth per row. The central and lateral teeth are tricuspidate. The simple, thorn-shaped marginal teeth consist of a narrow base and a recurved, almost lanceolate tooth in *Oxychilus* species (Fig. 17.61E). In *Zonitoides* species, the marginals are more peg-like (Fig. 17.61F). The similarity between the shells and reproductive anatomy of Australian specimens and of specimens from America described by Bartsch & Quick (1926) and Pilsbry (1948) indicated that *Zonitoides arboreus* was introduced into Australia (McLauchlan 1954; Bishop 1978). *Zonitoides* species have a dart sac which arises at the base of the penis. The dart sac has a bifurcate coronal gland attached to the duct of the bursa copulatrix which also has a diverticulum attached to the penis sheath (Fig. 17.61D). The morphology and histology of the alimentary and reproductive systems of *Oxychilus cellarius* were described by Rigby (1963) (Fig. 17.61C). She also detailed the breeding cycle of this species in Britain where laying takes place in spring with hatching about five to six weeks later. This is contrasted with *Oxychilus draparnaldi* which lays during autumn and early winter with hatching occurring the following spring. Little or no life history observations have been carried out on these introduced snails in Australia.

Zonitids are found mainly under well-watered garden and nursery conditions in temperate Australia. *Zonitoides arboreus* extends into subtropical and tropical areas of eastern Australia, where it feeds on mycelial threads in rotting timber; it is reported to cause damage to sugar-cane roots in North America (Bartsch & Quick 1926). Only one species, *Hawaii minuscula*, occurs in moist litter of forest and woodland areas. Though it is only found on Lord Howe and Norfolk Islands at present, it is anticipated that it will be recorded eventually from eastern Australia.

The source and purpose of odours produced by one or two zonitid species is not known. The most potent of these is the strong garlic smell produced by the garlic snail, *Oxychilus alliarius*, which is common in south-eastern Australia. It may be a protective mechanism.

Several of the species may be locally abundant, particularly in suburban gardens and nurseries. Because some of the commoner species feed on both living and moribund invertebrate animals, they are thought to be economically beneficial in these situations.

Family Trochomorphidae

Trochomorphid land snails are terrestrial and semi-arboreal. The shape of the small to medium-sized shell (usually 15–20 mm in diameter, occasionally larger), is lenticular to trochiform, or rarely discoidal or helicoid. Peripheral keels or carinal serrations are sometimes present. The shell sculpture is variable and consists of fine spiral striae and strong radial ribs or weak radial growth lines. The umbilicus is usually wide and the aperture may or may not have lamellae. Shell colour is variable. Supraperipheral and basal red bands are present in some species.

The only species recorded from Australia, *Trochomorpha melvillensis* (Fig. 17.62A–C), is restricted to Melville Island, Northern Territory (Solem 1988b; Smith 1992). The Polynesian and Micronesian trochomorphids were monographed by H.B. Baker (1941). Solem (1959a) discussed several Vanuatuan taxa (as New Hebridean). However, the absence of anatomical data on Papua New Guinean, Solomon Island and Indonesian taxa represents a large gap in the knowledge of the group.

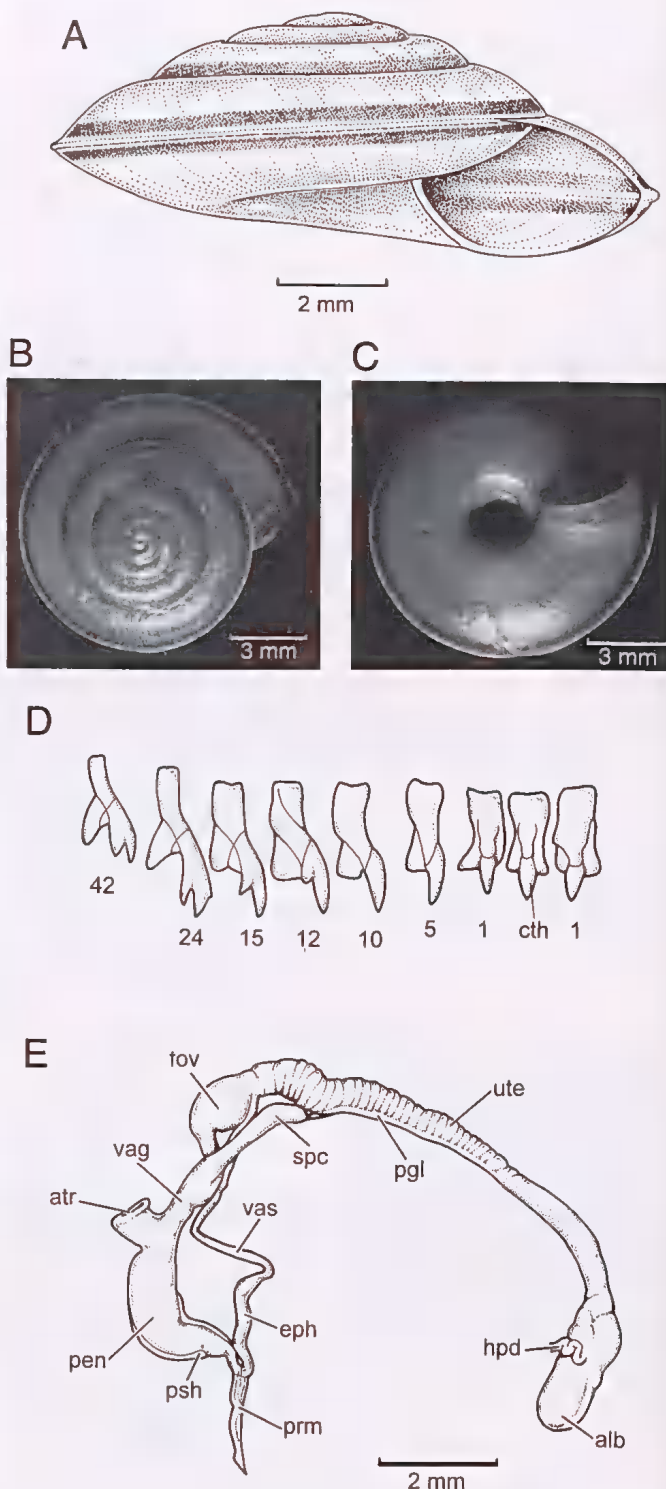


Figure 17.62 Family Trochomorphidae. *Trochomorpha melvillensis*, is restricted to Melville Island, Northern Territory, and is the only trochomorphid recorded from Australia. A–C, shells: A, apertural view; B, apical view; C, umbilical view. D, half of one radular transverse row; numbers denote position of tooth from the central. E, reproductive tract. alb, albumen gland; atr, atrium; cth, central tooth; eph, epiphallus; fov, free oviduct; hpd, hermaphroditic duct; pen, penis; pgl, prostate gland; prm, penial retractor muscle; psh, penis sheath; spc, spermatheca; ute, uterus; vag, vagina; vas, vas deferens. (D, after Bentham Jutting 1952; E, after Solem 1989)

[A, R. Plant; B, C, Queensland Museum; D, E, B. Scott]

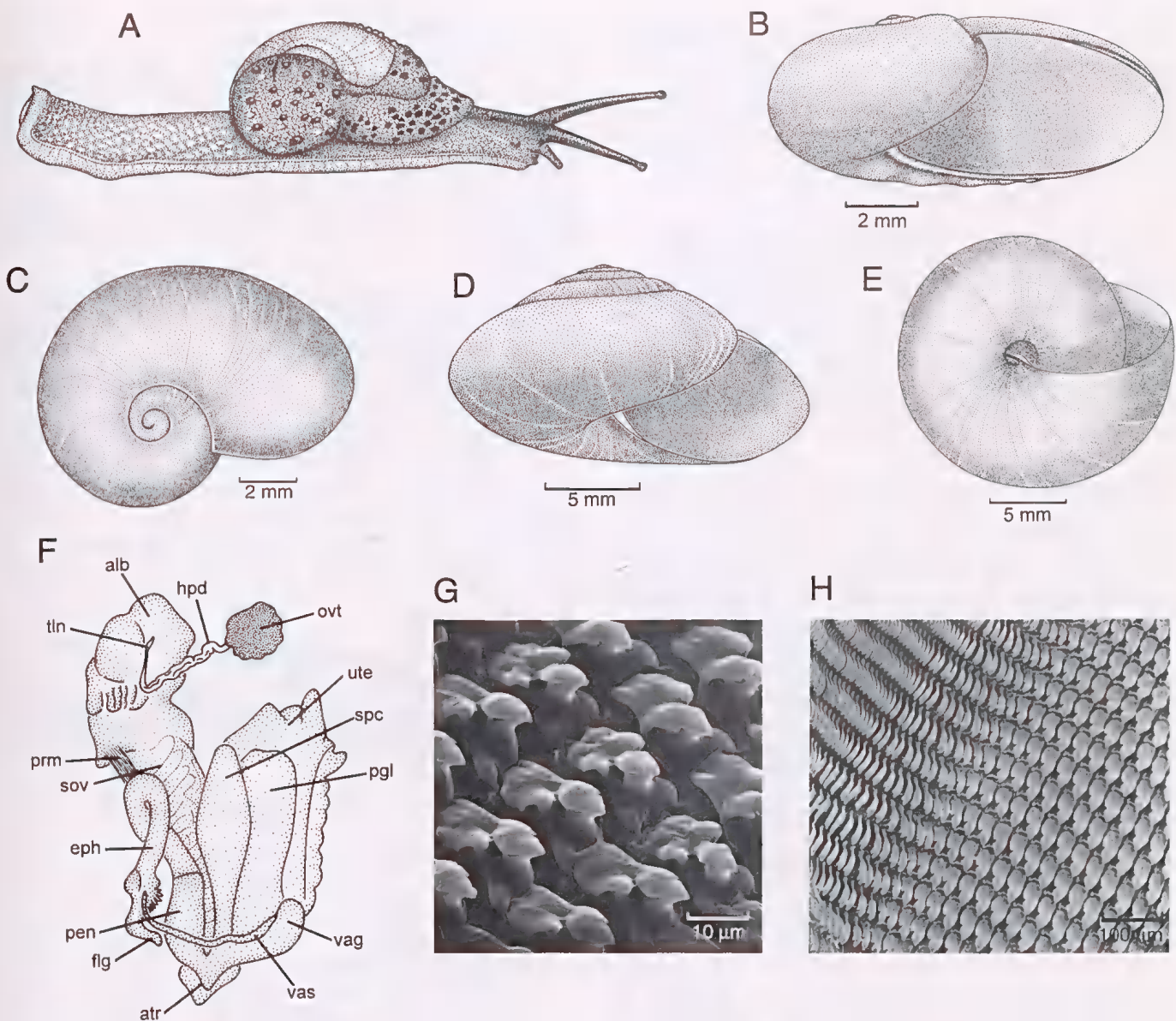


Figure 17.63 Family Helicarionidae. A, *Fastosarion aquila*, a semi-slug, crawling, showing the mantle flaps partially covering the reduced shell. B, C, *Helicarion cuvieri*, shell: B, apertural view, showing the wide aperture of the shell; C, apical view. D, E, *Nitor pudibunda*, shell: D, apertural view, showing the small aperture; E, umbilical view. F, *Helicarion cuvieri*, reproductive tract. G, H, portions of radulae: G, *Helicarion* sp.; H, *Nitor krefftii*. alb, albumen gland; atr, atrium; eph, epiphallus; flg, flagellum; hpd, hermaphroditic duct; ovt, ovotestis; pen, penis; pgl, prostate gland; prrm, penial retractor muscle; sov, spermatheca; tln, talon; ute, uterus; vag, vagina; vas, vas deferens. (A, after photograph by Queensland Museum; F, after Kershaw 1979)

[A–F, C. Eadie; G, H, B.J. Smith]

Anatomically, trochomorphids are characterised by a weak upper pedal groove and a foot sole that lacks divisions. The mantle does not have shell lobes and the lung lacks distinct secondary venation. The central and lateral teeth of the radula (Fig. 17.62D) have one to three cusps. The marginals are usually unicuspidate and sometimes bicuspidate. The jaw is smooth.

The trochomorphid penis lacks accessory appendages and the vagina is short (Fig. 17.62E). In *Trochomorpha melvillensis* there is a well-developed penial sheath around the upper half of the penis. Internally the penis has a large U-shaped stimulatory pilaster. The penial retractor muscle is inserted on the epiphallus (Solem 1988b).

Trochomorphids are either ground dwellers or arboreal. *Trochomorpha melvillensis* was found under the bark of trees.

Family Helicarionidae

Members of the Helicarionidae are ground-dwelling and arboreal terrestrial snails with small to medium-sized shells (about 3–30 mm in length) (Fig. 17.20D; Pl. 32.3); two basic forms occur in the Australian fauna. The shells may be very thin and

reduced compared to the size of the animal (Figs 1.61C, 17.63A) with few whorls and a very wide aperture (Fig. 17.63B, C) approaching the structure termed 'semi-slugs' by Solem (1974). Alternatively, they are low, conic and helicoid with up to five whorls which are large compared to the size of the animal (Fig. 17.63D, E). A few of the Australian species have been revised in recent years by Dartnall & Kershaw (1978), Kershaw (1979, 1981b, 1983), Solem (1982) and Stanisc (1988, 1993a, 1993d). Smith (1992) listed 107 species in 47 genera which included 51 species and 20 genera from Lord Howe Island and Norfolk Island. A single species, *Euconulus fulvus*, has been introduced into New South Wales (Stanisc 1981b).

The shells are dextral with weak, barely visible sculpture of fine spiral lines or the sculpture is absent. Reduced shells are transparent, often with a membranous base and no umbilicus. The animal has lappets which partly or nearly entirely cover the shell (Fig. 17.63A). The conic shells are small with a small to minute umbilicus which may have incised spiral lines within. A weak to bold peripheral keel is present in some species. The aperture does not have folds or teeth but the columella margin is more or less reflected. Helicarionids have an aulacopodous foot with a tripartite sole, two closely adjacent pedal grooves and a functional

17. PULMONATA

caudal gland commonly surmounted by a caudal horn. The mantle appendages may be reduced to small lobes. Caudal mucous colour differs between certain species or groups of species and may have significance in defence against predators. Body colours are simpler in most southern Australian species. Preliminary studies suggest a regional relationship in the distribution of these colour morphs, possibly associated with vegetation community type (R.C. Kershaw personal communication).

As far as is known most members of the family are herbivorous and several species have been observed to eat fungi. Grit is sometimes taken in with the food, possibly to assist digestion. The jaw has a medium projection. The radula bears tricuspidate central teeth, bicuspidate or tricuspidate lateral teeth and bicuspidate to multicuspidate marginal teeth (Fig. 17.63G, H). Typically, the radula has many teeth and some species have very large numbers of marginals. The kidney is narrow and curved to elongate with distinct primary and secondary ureters.

Helicarionids are protandric hermaphrodites. Australian species usually have no dart apparatus, but Odhner (1917) described at least one species from Queensland with this structure. The penis has an epiphallus and penial sheath. The simplest forms in south-eastern Australia have no retractor caecum, the flagellum is coiled and the free oviduct is very weakly glandular (Fig. 17.63F). The northern species commonly have a variable elongate, coiled retractor caecum, an elongate flagellum and a distinctly glandular free oviduct. Sperm are transferred in a spermatophore which may or may not be ornamented with complex spines. The elaboration of the flagellum to produce the spermatophore is a distinctive feature of these animals (Van Mol 1973). The small white calcareous-shelled eggs are laid in small clutches in litter and under bark. One or two of the species in northern Australia, related to forms in Indonesia and South-East Asia, may be ovoviparous (Smith & Djajasasmita 1988; Solem 1988b).

Helicarionids occupy a wide variety of habitats ranging from dry scrub and forest to temperate and tropical rainforest. Animals with reduced shells are confined to eastern Australia and the south-western corner of Western Australia. These species do not produce an epiphragm and require a moist environment for survival. This factor is probably responsible for the relatively restricted distribution in Australia. The conic forms are widespread throughout the continent except for very arid regions and grasslands. Arboreal species occur in New South Wales, Queensland and on Lord Howe and Norfolk Islands. Predators include birds and species of the carnivorous snail family Rhytididae. Aestivation occurs during dry periods. The marsupial lungworm has been recovered from the Queensland species *Helicarion virens* (see Spratt 1979). Helicarionids have no known economic value.

The family, as presently understood, includes about 150 genera with a range centred on southern and eastern Asia, Australia and the central and western Pacific. However, a few groups of genera, which may be considered subfamilies, are found in Africa and Europe, with a few species as world travellers (Smith 1989). Differing views on the limits and relationships of the family have been put forward by Solem (1966), Van Mol (1973) and Bishop (1981). Thirty-three of the 35 Australian genera are endemic. Many of these are of small conic species found mainly on Lord Howe Island (for example, in the genera *Innesoconcha*, *Mathewsoconcha*, *Gudeoconcha*, *Epiglypta*) and Norfolk Island (for example, *Roybellia*, *Fanulena*). The few found on mainland Australia are mainly confined to the tropical and subtropical areas (for example, species of *Fastosarion*, *Thularion*, *Malandena*, *Nitor*). The different forms of *Helicarion*-like species may be derived from successive waves of colonisation from South-East Asia and Papua New Guinea, probably via the forested coastal regions of eastern Queensland and New South Wales in southern Australia (Solem 1959b).

Family Cystopeltidae

Members of the family Cystopeltidae are small to medium terrestrial slugs (10–35 mm body length) with a large visceral mass, covered by a shield-like mantle, which is separate from the tail posteriorly (Fig. 17.58A). They have a very thin, horny, internal shell. The truncate tail has a variable chevron pattern above and has a distinct, functional caudal gland. The anatomy has been described by Hedley (1890), Davies (1912), Kershaw (1987b) and Daniell (1991). Smith (1992) lists four species for the Australian fauna.

The animal is a slug with a soft visceral mass separated from the tail posteriorly (Fig. 17.64A), a body form seen in no other family of slugs. All species in the family show a similar general body form but differ in size, body colour and internal anatomy. The stomach, intestine and much of the reproductive system remain in the visceral mass, which forms a distinct hump as in most shelled snails. The head-foot contains the oesophagus and salivary gland, the terminal genitalia and the basal lobe of the apical gonoduct. The foot is aulacopodous, with a distinct pedal groove, and a sole which may be patterned but is not tripartite. The jaw is very thin, flexible and faintly sculptured. The radula (Fig. 17.64D) has a very large number of minute teeth (over 300 per row) with

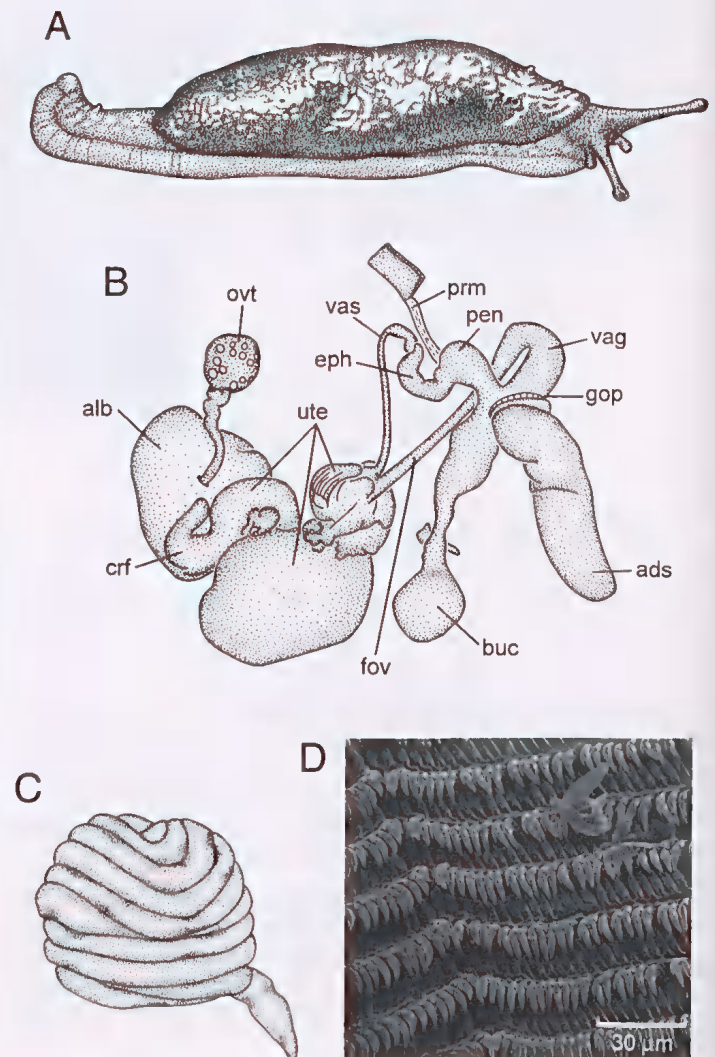


Figure 17.64 Family Cystopeltidae. A, *Cystopelta* sp., crawling animal showing the distinctive body shape. B, *Cystopelta petterdi*, reproductive tract. C, characteristic cystopeltid faecal coil found on the trunks of trees. D, *Cystopelta* sp., portion of radula. ads, atrial duct sheath; alb, albumen gland; buc, bursa copulatrix; crf, carrefour; eph, epiphallus; fov, free oviduct; gob, gonopore; ovt, ovotestis; pen, penis; prm, penial retractor muscle; ute, uterus; vag, vagina; vas, vas deferens. (A, after photograph by Queensland Museum; B, after Kershaw 1987b)

[A–C, C. Eadie; D, A. Daniell]

unicuspidate or tricuspidate central teeth, tricuspidate lateral teeth and multicuspidate marginal teeth, mounted on distinctly elongate basal plates (Kershaw 1987b; Daniell 1991). The kidney is somewhat oblong. The eyes are situated on long optic tentacles which have very wide bases. The inferior sensory tentacles are also long with wide fleshy bases.

Individuals are protandric hermaphrodites, and animals alternate as male and female during copulation (Daniell 1991). There is no flagellum or dart sac but the vas deferens expands into an epiphallus (Fig. 17.64B). The talon, or seminal receptacle, consists of two simple lobes adjacent to the globular ovotestis (Kershaw 1987b). These lobes swell with sexual maturity. Mating occurs in spring and summer. The oviducal pore is elongated in *Cystopelta petterdi* forming a cone-shaped process which is used to stroke the penis of the partner. Sperm are transferred in a simple spermatophore. The small spherical, almost transparent, eggs are laid scattered singly under or inside rotting logs in both spring and autumn. Hatching is thought to occur within 10–20 days under favourable conditions (Daniell 1991).

Cystopeltids are found in forest areas, usually in damp conditions but can be found in wet and dry sclerophyll forest and in alpine snow-gum woodland. They are semi-arboreal and readily climb up the trunks of trees in damp or wet conditions (usually only at night). They seek shelter under logs and in the litter and loose soil in drier conditions. Many forms appear to be cryptically coloured, with a light and dark mottled appearance which closely resembles the tree trunk on which they are observed. Under favourable conditions, large populations have been observed active on trees, particularly in Victoria and Tasmania (Allan 1950; Smith 1980) and the Blue Mountains, New South Wales (W.F. Ponder personal communication). The animals are thought to feed on the minute lichens and bacterial film on tree trunks (Daniell 1991). The faeces are ejected in a characteristic ribbon coil (Fig. 17.64C), and their presence on tree trunks indicates occurrence of these animals in an area. Animals often seek shelter in the long coiled streamers of free-hanging bark in wet eucalypt forests.

The main predators are probably birds and rhytidid snails (Smith 1980). Feeding is a nocturnal activity under wet conditions in dry forests, but in dense wet forests the animals are active during the day. The animal secretes a green caudal mucus when the foot is irritated. Observations suggest that the colour of both mucus and foot may vary with the season, age and vegetation type. The mucus secreted by cystopeltids fluoresces under ultra-violet light (Daniell 1991), but neither its function nor its significance is known.

This endemic family is confined to eastern Australia, from Tasmania to southern Queensland. *Cystopelta* is the only genus in the family. Two species are recorded from Tasmania (*C. bicolor* and *C. petterdi*), one from southern New South Wales and Victoria (*C. astra*) and one from Queensland to Victoria (*C. purpurea*) (Iredale 1937b; Smith 1992). Daniell (1991, 1994) implied that more species are yet to be described.

The affinities of the family to other molluscan groups are uncertain (Kershaw 1987b). Hedley (1893) compared the animal of a *Cystopelta* species, with the helicarionid *Parmacochlea fischeri*. Bishop (1981) stated that a derivation from a helicarionid is unlikely. The ureter is much modified and is not obviously sigmurethran. However, a sigmurethran ancestor seems most probable (see Solem 1978a for discussion). Based on similarities in the structure of the digestive and nervous systems, Tillier (1989) aligned the family more closely with the Endodontoidea.

Family Testacellidae

Testacellids are very unusual slugs, which are easily recognised by the elongate slug-like body and the small, auriculiform shell located at the posterior end (Fig. 17.65A). The family is native to western Europe but has been introduced accidentally into many parts of the temperate world, including southern Australia (Smith & Kershaw 1979; Smith 1989). A detailed description was given by Quick (1960).

The sub-cylindrical body tapers towards the anterior end and extends to about 130 mm in length. The shell, located at the posterior extremity, is reduced to an oval to auriculiform remnant about 10 mm in length with a tiny, posteriorly pointing apex. The small mantle is situated posteriorly and covers a portion of the shell. Two grooves lead forward from the mantle on the upper lateral surfaces from which oblique side branches descend on each side. These are thought to be concerned with mucous secretion, possibly associated with feeding. The foot is aulacopodous with peripodal furrows but lacks a caudal mucous pit or gland. The pedal gland is free in the body cavity. The pericardium is on the right side of the kidney with the ventricle in front of the auricle. The kidney lacks a distal secondary ureter, and the primary ureter opens deep in the pulmonary cavity.

Testacellids are carnivorous and prey on earthworms which they grasp rapidly with the radula and smother with body mucus. The prey is ingested rapidly. Most of the features of the alimentary system and many of the general body features are adaptations to the carnivorous habit. These include the absence of jaws, the large, muscular buccal mass with a modified radula, the short and simple digestive tract. The posterior location of the respiratory opening provides for a long, unrestricted head region. The radula consists of about 50 sharp V-shaped rows of teeth (Fig. 17.65C). The teeth are simple and lanceolate. The central tooth is weak or absent. The lateral teeth increase in size laterally, reaching a maximum after some 10 to 12 teeth from the centre, and declining in size through the marginal teeth (Quick 1960). This pattern is very similar to the arrangements in other unrelated carnivorous groups (Smith 1987).

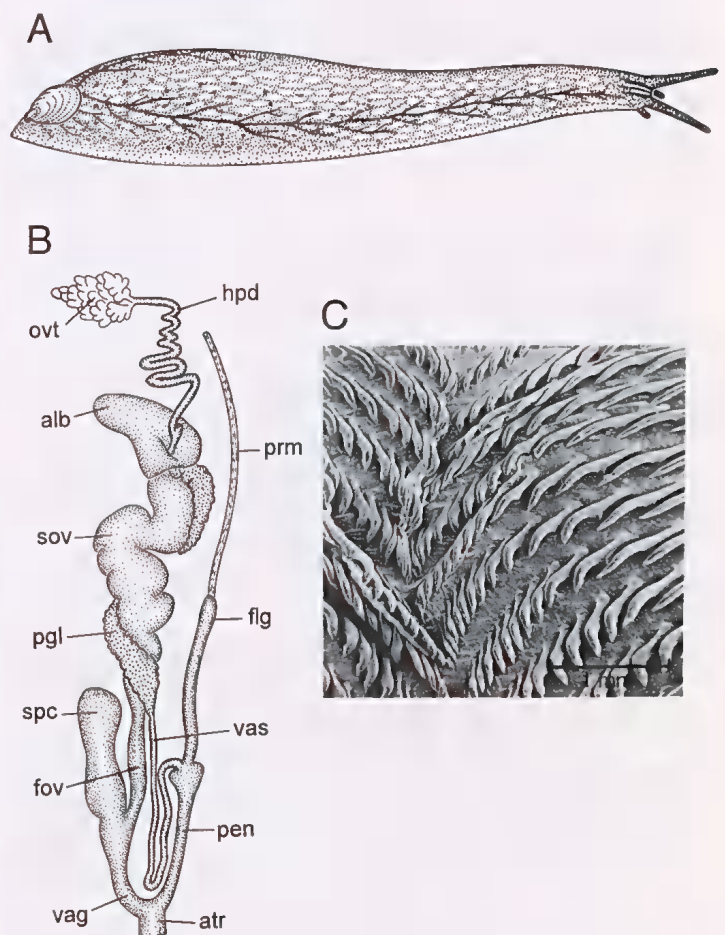


Figure 17.65 Family Testacellidae. *Testacella halionidea*: A, crawling animal showing the reduced, posteriorly placed shell; B, reproductive tract; C, portion of radula. alb, albumen gland; atr, atrium; flg, flagellum; fov, free oviduct; hpd, hermaphroditic duct; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; sov, spermoviduct; spc, spermatheca; vag, vagina; vas, vas deferens. (A, after Kerney & Cameron 1979; B, after Quick 1960) [A, B, C. Eadie; C, B.J. Smith]

17. PULMONATA

Testacellids are protandric hermaphrodites. The thin, elongate penis has a flagellum and a well-developed retractor muscle (Fig. 17.65B). A short duct is sometimes seen between the penis and vagina and is thought to facilitate self-fertilisation. The eggs are large and ellipsoidal (7×4 mm in *T. haliotidea*), with a calcareous shell. They are laid in batches of two to 14 eggs and take four to five months to hatch (Quick 1960).

Individuals spend much of their lives burrowing in moist soils of high organic content, where their prey are plentiful. For this reason they are associated with gardens and are seldom seen. They have little economic significance because they are comparatively rare. Nevertheless, they appear to have the adaptability to be successful world travellers (Smith 1989). The family contains only one genus, *Testacella*, with about five or six species. Several of these have been introduced into various parts of the world. Only one species, *Testacella haliotidea*, is confirmed for Australia (Smith & Kershaw 1979) and this has only been recorded occasionally from the main population centres of Sydney, Melbourne and Hobart.

Superfamily SUCCINEOIDEA

The position of the two morphologically distinct families included in the Succineoidea among the Sigmurethra has yet to be unequivocally established. These families – the Succineidae and Athoracophoridae – have often been placed in their own ordinal divisions, the Heterurethra and Tracheopulmonata, respectively. Solem (1978a) thought that the Succineidae were Sigmurethra with a peculiar habitat, and that the aberrant tracheopulmonate slugs of the Athoracophoridae were sigmurethrans that became ‘weirdly sluggish’. Their relationships to other shelled sigmurethran groups have not yet been determined and hence the grouping under a single superfamily should be regarded more as one of convenience rather than indicating any close kinship. Tillier (1989) considered the Athoracophoridae to be an endodontoid family and placed the Succineidae with the Achatinoidea, however this arrangement is not universally accepted.

The two families are characterised by their peculiar, highly modified pallial cavities, their unusual ureter and kidney configurations and their elasmognathous jaws. Both occur in Australia.

The Athoracophoridae are large slugs without an external shell (Fig. 1.61D). They are restricted to Queensland, New South Wales, Papua New Guinea, the Bismarck Archipelago, Vanuatu, New Caledonia and New Zealand. In contrast, the Succineidae are a cosmopolitan family of small thin-shelled molluscs associated with moist habitats (Solem 1959a).

Family Succineidae

Succineid snails often are associated with marshes and swamps in wetter climates, and they live near waterfalls on many Pacific Islands. They also inhabit sand dunes and seasonally dry stream banks in many regions. With very few exceptions, the shell has a greatly reduced whorl count and a very capacious last whorl (Fig. 17.66A, B). In a few taxa, the shell is reduced to an oval plate and is much smaller than the animal. The shell lip is always thin and not expanded. The shell usually is light yellow or greenish horn in colour in wetter areas; it becomes lighter or even white under dry conditions. Usually the snail’s body can be withdrawn into the shell, except when the latter is reduced to a fragment. Some succineids are semi-slugs with their shells reduced; some species have shells that resemble a small plate. The head and neck are very short, a state reflected in structural changes to several organ systems, as summarised by Solem (1978a). Frequently the body and/or the mantle has conspicuous black markings. The jaw is elasmognathous, with a greatly enlarged attachment plate.

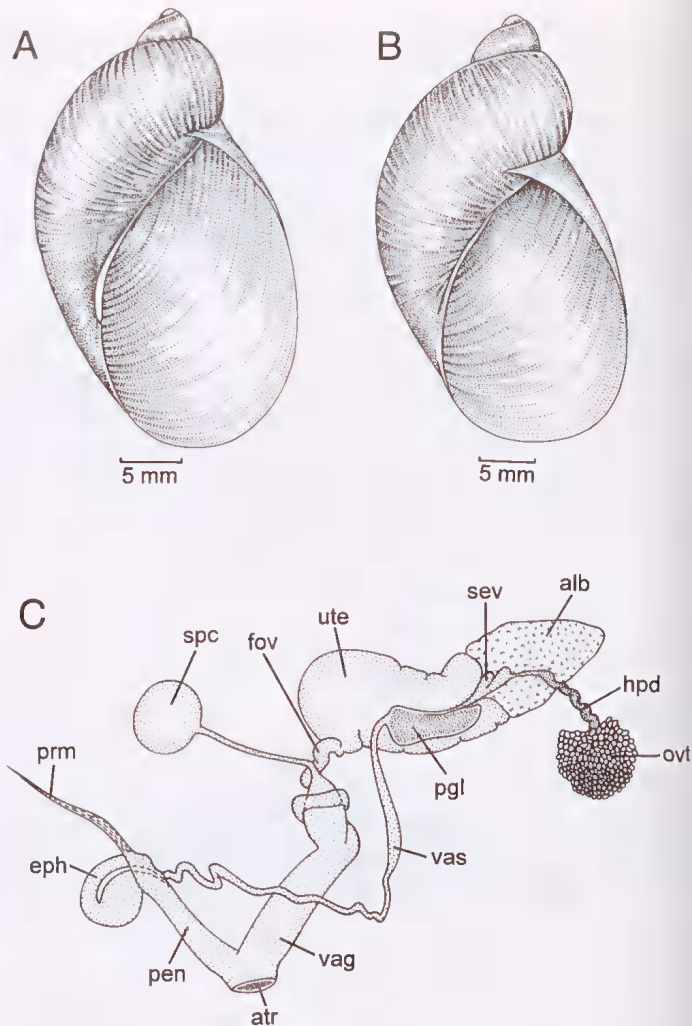


Figure 17.66 Family Succineidae. A, B, shells, apertural view: A, *Succinea scalarina*; B, *Succinea australis*. C, *Succinea ovalis*, reproductive tract. alb, albumen gland; atr, atrium; eph, epiphallus; fov, free oviduct; hpd, hermaphroditic duct; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; sev, seminal vesicle; spc, spermatheca; ute, uterus; vag, vagina; vas, vas deferens. (C, after Solem 1976)

[A, B, R. Plant; C, C. Eadie]

No comprehensive monograph of the Succineidae exists. Patterson (1971) gave a synoptic review of genera, but did not work directly with Australian taxa. A number of Australian species and two genera, *Austrosuccinea* and *Arborcinea*, have been named (Iredale 1937a, 1939), and there have been few subsequent listings in faunistic reports (summarised in Solem 1988b). North American taxa have been reviewed by Pilsbry (1948) and Hoagland & Davis (1987). Quick (1933, 1936) presented anatomical data on British and African species, respectively; the reproductive anatomy of a succineid, *Succinea ovalis*, is illustrated in Figure 17.66C. Though a number of Australian endemic species probably exist, none have been defined and diagnosed adequately. Smith (1992) listed seven species in the genus *Succinea* from Australia, including *S. norfolkensis* from Norfolk Island.

The Australian distribution of succineids is sporadic, with a surprising abundance of colonies in central Australia, the Gawler Ranges of South Australia, and occasionally in Western Australia. They are common in both Victoria and Tasmania.

Powell (1950) provided extensive details on the life history of the New Zealand *Austrosuccinea archeyi*. However, nothing is known of the life history of any Australian species. Smith & Kershaw (1979) and Solem (1988b) suggested that *Arborcinea* (found under bark in dry forests) is based on aestivating juveniles of *Succinea*. Both Patterson (1971) and Solem (1988b) suggest that *Austrosuccinea* is probably not a valid genus. Succineids are not known to be of any economic importance.

Family Athoracophoridae

The small to large slugs of the Athoracophoridae have shells which are reduced to several internal calcareous fragments (Fig. 1.61D). The dorsal surface of the animal is divided into a triangular mantle, cephalic shield and notum (Fig. 17.67A; Pl. 32.5). These regions are covered by a usually well-developed network of slime furrows. The pallial cavity is reduced and the lung consists of trachea-like tubules and air spaces.

A single genus *Triboniophorus* occurs in eastern Australia and Papua New Guinea (Fig. 17.67A), and a further three genera occur in New Caledonia and Vanuatu (*Aneitea*), New Britain and the Admiralty Islands (*Aneitiella*), and New Zealand, including neighbouring islands (*Athoracophorus*). Solem (1959a) concluded that there is only one Australian species, *T. graeffei*, which ranges from the Illawarra region, New South Wales, through coastal Queensland to Papua New Guinea. This opinion was supported by Burton (1980), who carried out detailed anatomical studies on various geographic populations of *T. graeffei*, and by Smith (1992). Hedley (1889b) examined the relationships of *T. graeffei* and provided the first details on its anatomy.

Triboniophorus graeffei varies considerably in colour. The most common form has a light bluish-grey to white, or creamy-yellow base colour. Red pigment surrounding the mantle triangle and along the edges of the foot give rise to the common name, red-triangle slug. However, there are numerous colour variations on this basic pattern, particularly in montane regions. In the New England National Park, northern New South Wales, colour variation is extreme and differing degrees of reddish-pink suffusion occur over the entire body. At Mt Kaputar, near Narrabri, New South Wales, the whole body is a spectacular bright red colour. On the heights of Mt Bellenden Ker, North Queensland, *T. graeffei* is bright orange, and a completely white form has been collected on neighbouring Mt Bartle Frere. The slug may reach 170 mm in length.

The shell of *T. graeffei* consists of a number of fragments situated under the epidermis of the mantle shield (Hedley 1889b). The jaw is elasmognathous and has a squarish support cartilage and two well-developed 'wings' with reflexed lateral margins (Fig. 17.67C). The central tooth of the radula in *Triboniophorus* is reduced in size and has three to five cusps (Fig. 17.67B). The lateral teeth have two to four platelike cusps; similar but larger cusps occur on the marginal teeth. In contrast *Aneitiella* has no central tooth. The excretory system of athoracophorids is unusual in having a highly convoluted ureter. Four to five loops are present in *T. graeffei*. A characteristic feature of the family is the highly unusual pallial system in which the typical pulmonate lung is replaced by a lung with trachea-like air spaces. The penis is elongate and highly coiled. The oviduct is elongate and has an accessory oviducal gland at the posterior end (Fig. 17.67D).

Burch (1968) showed that tentacular structure and mode of tentacle retraction in the Athoracophoridae differ from those of other Stylommatophora, which led Burch & Patterson (1969) to suggest that this family is related to the Succineidae. Solem (1978a) considered that the highly folded sigmurethrous ureter and high chromosome number (Burch & Patterson 1971b) of the Athoracophoridae indicates an aberrant group. Nevertheless, he maintained the two families in a separate superfamily, the Succineoidea.

Triboniophorus graeffei is found in moist and dry sclerophyll forest and rainforest. Usually it lives buried in the ground or under logs and rocks during the day. At night, especially after rain, individuals can be found feeding on the surfaces of smooth-barked trees (often *Eucalyptus* species) where their tell-tale rows of circular feeding tracks may be seen if the slug is in residence. Mt Kaputar individuals feed on the surface of huge granite boulders.

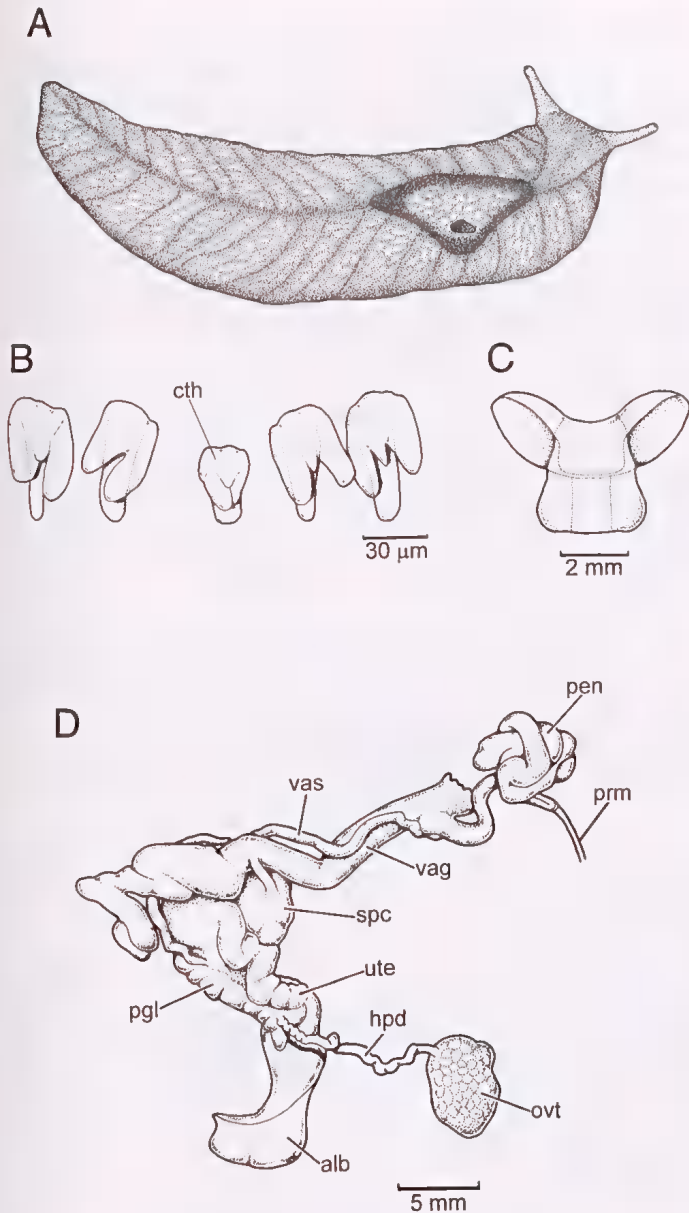


Figure 17.67 Family Athoracophoridae. *Triboniophorus graeffei* is the only member of this family in Australia. A, crawling animal, showing the characteristic triangular mantle area with the pneumostome; B, portion of radular transverse row showing the central tooth with the first two lateral teeth either side; C, jaw; D, reproductive tract. alb, albumen gland; cth, central tooth; hpd, hermaphroditic duct; ovt, ovotestis; pen, penis; pgl, prostate gland; prm, penial retractor muscle; spc, spermatheca; ute, uterus; vag, vagina; vas, vas deferens. (A, after photograph by Queensland Museum; B–D, after Burton 1980) [A, C. Eadie; B–D, B. Scott]

The Succineidae have a nearly worldwide distribution. At present, all Australian species are treated as belonging to the genus *Succinea*. Undoubtedly this will change when the Australian species are studied in detail. The lowest number of chromosomes reported for any land snail group distinguishes the genera grouped in the subfamily Catinellinae. Whether this in some way reflects an ecological adjustment to ephemeral habitats (as proposed by Solem 1978a and previously) or represents a primitive condition (references in Patterson 1971) is still unsolved. Unusual morphological features of the animal have been interpreted very differently, and the Succineidae have been placed variously in the Opisthobranchia (Rigby 1965), separated at the ordinal level although retained within the Pulmonata, or placed as a superfamily in the Aulacopoda (see summary and references in Solem 1978a).

There is no useful fossil record of succineids in Australia. However, they are known from Tertiary deposits in Africa, Europe (Zilch 1959) and North America (Hoagland & Davis 1987).

Based on radular features, Solem (1959b) suggested that the Athoracophoridae arose in the north and spread south. Previously Grimpe & Hoffman (1925b) postulated an Antarctic origin followed by two northward radiations. Burton (1980) concluded that the radiation and speciation of the New Zealand taxa mask original distribution patterns to such an extent that resolution of this biogeographical problem is no longer possible.

Superfamily POLYGYROIDEA

Members of this superfamily have a very small to medium-sized shell which is discoidal, lenticular or globosely conic in shape. The umbilicus varies from closed to widely open and cup-shaped. The peristome (lip) is often thickened and sometimes the aperture is partially occluded by denticles and lamellae. The foot is holopodous. The radula usually has a tricuspidate central tooth, bicuspidate lateral teeth and variable marginal teeth. The penis is simple or has a flagellum; a penial sheath may be present or absent. There is no epiphallus.

Three families are included, following Solem (1978a). These include the largely North American Polygyridae, and the Sagdidae from southern North America, Central America and the Antilles. The third family, the Corillidae, is found in South-East Asia (especially China), India, Africa and Australia. Very few genera are recognised and only a single monotypic genus occurs in Australia.

Family Corillidae

Corillids are characterised by a shell which is very small to medium in size, discoidal or planispiral, and usually has a wide open umbilicus. The shell is dextral or sinistral and numbers of whorls vary from four to eight. The lip is usually thickened and the aperture often has teeth or lamellae.

Only a single species, *Craterodiscus pricei*, has been recorded from Australia (Fig. 17.68A–C). It is known only from a few localities in the Wet Tropics of north-eastern Queensland, where it lives among volcanic gravel. The family contains five genera and has no known fossil record.

McMichael (1959) inferred that *C. pricei* may be a helicarionid because of its reduced sculpture. Solem (1973) provided detailed information on shell, radula and reproductive anatomy of *C. pricei* and placed it in the Camaenidae. Tillier (1989) placed the species in the Corillidae because it lacks an oesophageal crop, absent in all corillids but present in camaenids. This opinion is followed here in preference to that of Smith (1992) who retained this species in the Camaenidae.

The shell of *C. pricei* is small (5–6 mm in diameter) with a high whorl count (6–6.5 whorls). The umbilicus is wide open and the shell sculpture is reduced. The lip is simple and the aperture lacks apertural lamellae or denticles. The combination of high whorl counts and a small cross-sectional whorl area has led to noticeable elongation of all organ structures (Solem 1973). The

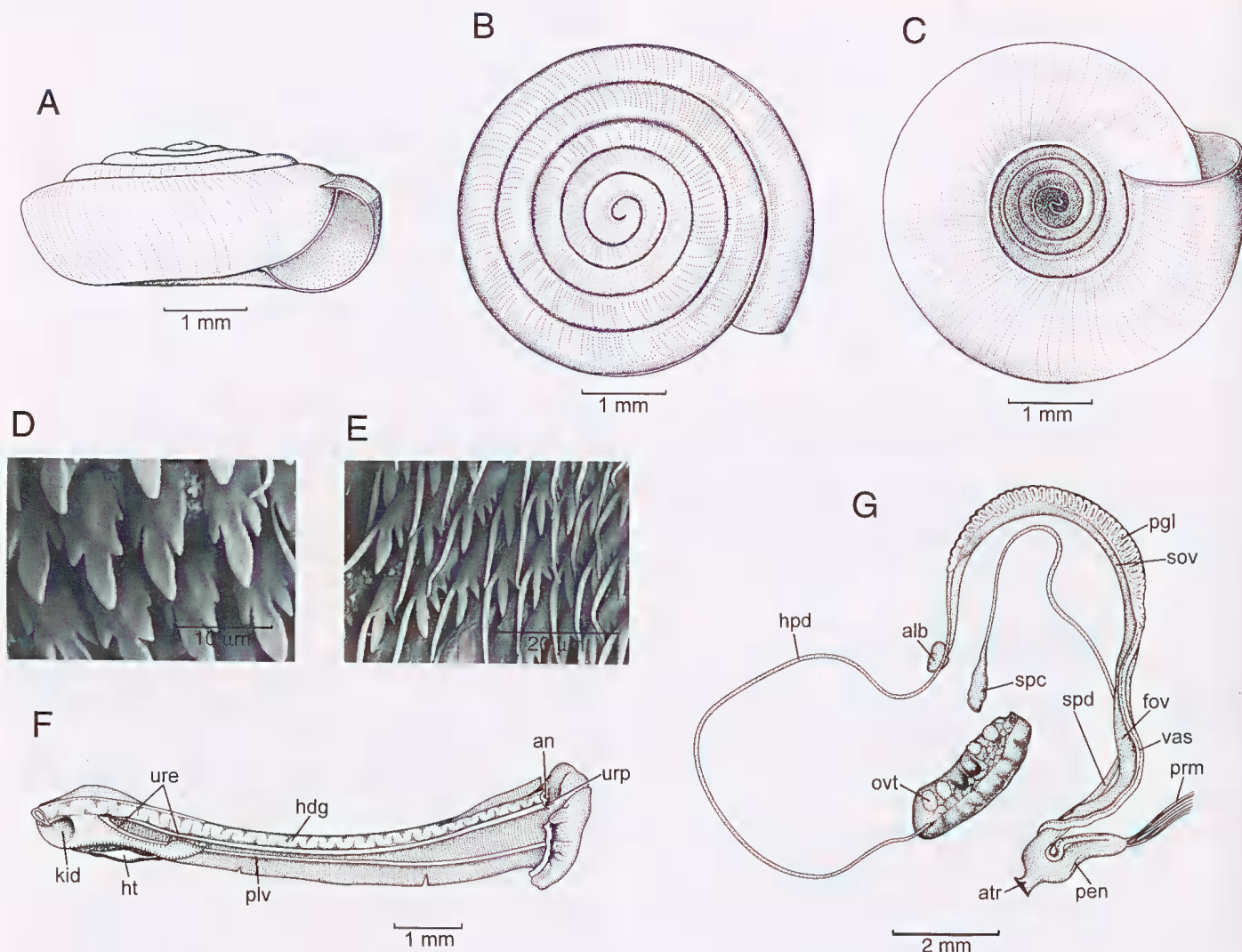


Figure 17.68 Family Corillidae. *Craterodiscus pricei*. A–C, shell: A, apertural view; B, apical view; C, umbilical view. D, E, portions of radula: D, details of central and lateral teeth; E, outer marginal teeth. F, pallial region. G, reproductive tract. alb, albumen gland; an, anal pore; atr, atrium; fov, free oviduct; hdg, hindgut; hpd, hermaphroditic duct; ht, heart; kid, kidney; ovt, ovotestis; pen, penis; pgl, prostate gland; plv, pulmonary vein; prm, penial retractor muscle; sov, spermoviduct; spc, spermatheca; spd, spermathecal duct; ure, ureter; urp, ureteric pore; vas, vas deferens. (A–C, after McMichael 1959; F, G, after Solem 1973)

[A–C, A.J. Hill; D, E, Queensland Museum; F, G, C. Eadie]

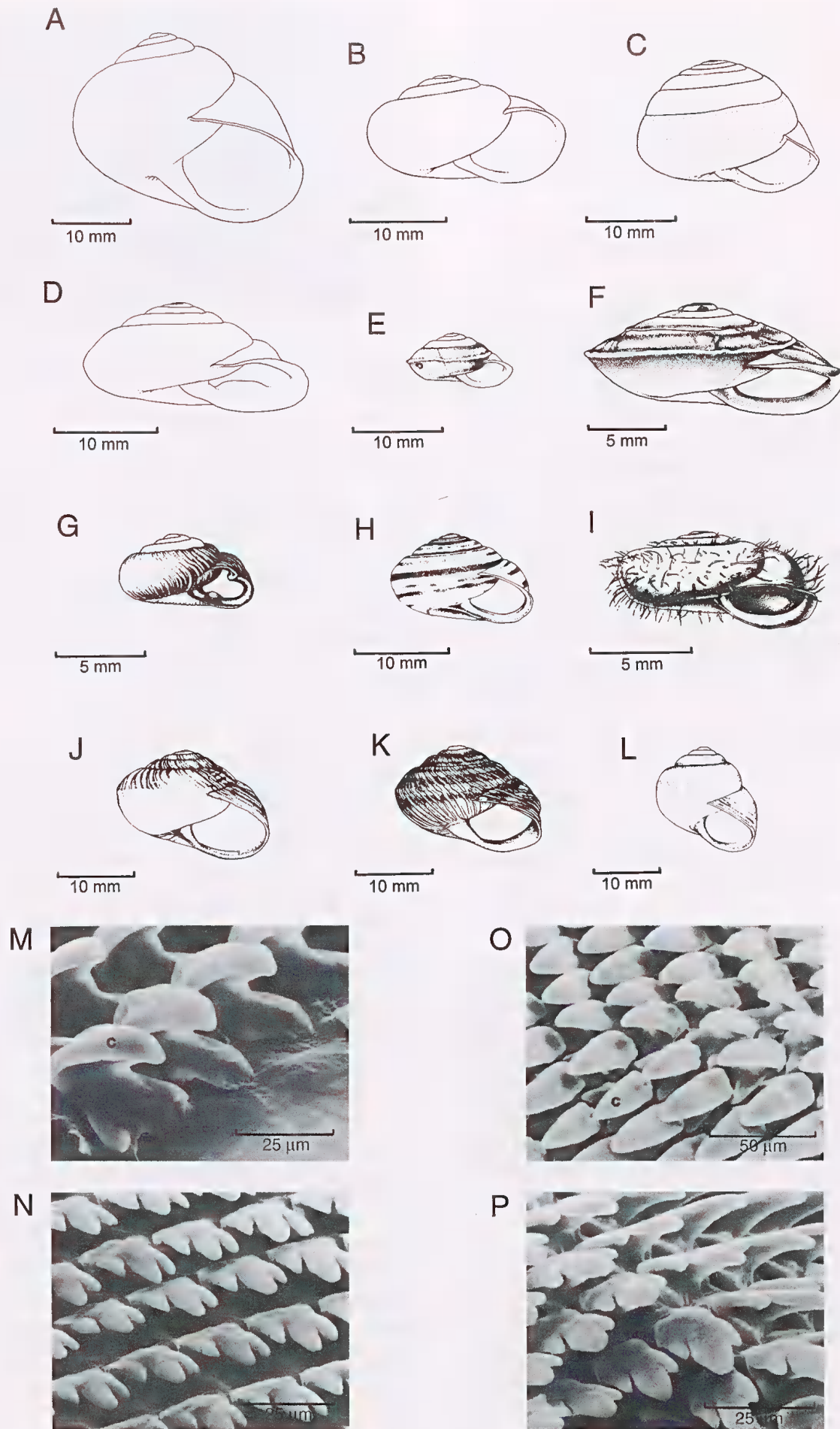


Figure 17.69 Family Camaenidae. This is the most widespread and diverse land snail family in Australia. A–L, shells, apertural view: A, *Xanthomelon obliquirugosum*; B, *Torresitrachia torresiana*; C, *Amplirhagada elevata*; D, *Cristilabrum grossum*; E, *Westraltrachia froggatti*; F, *Ordtrachia grandis*; G, *Baudinella regia*; H, *Rhagada harti*; I, *Damochlora spina*; J, *Cupedora sutitosa*; K, *Glyptorhagada silveri*; L, *Sinumelon bitaeniatum*. M–P, portions of radulae: M, N, *Westraltrachia porcata*, mid-angle side view of central and early lateral teeth (M) and mid-angle front view of outer marginals (N); O, *Westraltrachia subtila*, central and lateral teeth; P, *Westraltrachia instita*, teeth at the latero-marginal transition. (M–P, from Solem 1984)

[A–L, A. Solem]

17. PULMONATA

pallial region extends about one whorl apically and the kidney is compact (Fig. 17.68F). The pulmonary vein is directed away from the hindgut and pneumostome. *Craterodiscus pricei* has a simple reproductive system without a penial appendix; spermatophores are formed. There is relatively little fusion of the male and female tracts and the hermaphroditic duct is elongate (Fig. 17.68G).

The radula of *C. pricei* has a tricuspidate central tooth. The lateral and marginal teeth have peculiar endoconal prolongations (Fig. 17.68D, E; Solem 1973).

Superfamily CAMAENOIDEA

Camaenoidean land snails have small to relatively large shells (60–70 mm in height or diameter). The shell shape is variable and ranges from discoidal to helicoid, trochiform to ovate-elongate. The shell sculpture is variable and periostracal setae are present in several groups. The aperture is usually open but in some genera a complex arrangement of lamellae has developed. The peristome is generally thickened and reflected. The jaw is smooth or striate. The radula (Fig. 17.69M–P) has a weakly tricuspidate central tooth with reduced ectocones. The lateral teeth are bicuspidate through reduction or loss of the endocone and enlargement of the ectocone and the marginal teeth tend to be multicuspidate as a result of endoconal enlargement and ectoconal splitting (Pilsbry 1939; Solem 1984b). Modifications of this pattern are many and include changes to the inter-row support system through the development of an anterior flare on the tooth margin (Solem 1984b). The kidney is usually long and tapered. The ureter is typically sigmurethrous and may be open or closed. Camaenoideans are hermaphrodites and oviparous. The reproductive system usually includes accessory appendages, an epiphallus on the male side, and, in Ammonitellidae only, a sac-like structure at the vagina/free oviduct junction.

Only two families are included. The Ammonitellidae are a small ancient group from the western United States. The Camaenidae are the dominant land snail family in most parts of Australia. Elsewhere camaenids have a disjunct distribution and are diverse in South-East Asia, Japan, the Philippines, New Guinea, the Solomon Islands, the Greater Antilles, Costa Rica and Bolivia. Fossil camaenids have been found in Cretaceous deposits in the United States (Solem 1978b).

Family Camaenidae

Camaenids (Fig. 17.70; Pls 32.1, 32.2) are the dominant land snails over most of Australia in respect to both diversity and biomass of molluscs at a given locality. The family is of northern origin, probably colonising and radiating in Australia over the same period as did the rodents. Although most Australian species are terrestrial, a few arboreal Indonesian (*Amphidromus cognatus*; Solem 1983b) or New Guinea-Melanesian (*Papuina sensu lato*; Iredale 1938) taxa inhabit the wet parts of the Northern Territory and Queensland. Semi-arboreal taxa also occur in the wet areas of Queensland and northern New South Wales. Maximum shell dimension varies from 5–100 mm. Shell colour ranges from bright and varied in wet area taxa, through brownish-yellow with or without spiral bands to almost white in arid zone taxa. Relative body size and colour vary greatly, usually in relation to habitat. Most species have a generalised jaw and radula, but there are repetitive specialisations that correlate with dietary shifts, especially in semi-arid areas when two or more camaenid species are sympatric, and in most arboreal taxa.

No comprehensive monograph of the Australian camaenids exists. In his checklist, Iredale (1937b, 1938) divided this complex into several families which have not been accepted by subsequent workers. Smith (1992) lists over 300 camaenid species, many of which have been revised in recent monographs from the Kimberley (Solem 1979b, 1981b, 1981c, 1984b, 1985a, 1988c), southern South Australia (Solem 1992), central Australia (Solem 1993) and non-Kimberley portions of Western Australia. Probably an equal number inhabit the eastern states and the Northern



Figure 17.70 Family Camaenidae. *Adclarkia dawsonensis*, an eastern Australian camaenid from south-eastern Queensland. [Queensland Museum]

Territory north of the Roper River. Stanisc (1996a, 1996b) described two new monotypic genera from Queensland. A total camaenid fauna of 700 to 800 species is highly probable. Generic and subfamily classification are still unsettled, with half the genera not yet assignable to subfamily units. The subfamilies recently delineated (Solem 1992, 1993) include the restricted endemic Sinumeloninae, and the Camaeninae which extends from South China to the Solomon Islands, Queensland and New South Wales, with a western radiation in the Flinders and Gawler Ranges of South Australia. The Pleurodontinae occur in central Australia, along the west coast of Australia from Carnarvon to the Mitchell Plateau, and in the West Indies.

Shell form is deceptively simple, and multiple convergences are evident in different subfamily units. Perhaps the nearest to average shapes are shown by *Torresitrachia torresiana* (Fig. 17.69B) and *Damochlora spina* (Fig. 17.69I). Higher spire form can be attained by doming (*Amplirhagada*, Fig. 17.69C) or spire elongation (*Xanthomelon*, Fig. 17.69A; *Sinumelon*, Fig. 17.69L). Angulate or keeled peripheries (*Cristilabrum grossum*, Fig. 17.69D; *Westraltrachia froggatti*, Fig. 17.69E; *Ordtrachia grandis*, Fig. 17.69F; *Glyptorhagada silveri*, Fig. 17.69K) have evolved many times. Apertural barriers are highly varied (*Cristilabrum grossum*, Fig. 17.69D; *Baudinella regia*, Fig. 17.69G), as is shell sculpture (*Baudinella regia*, Fig. 17.69G; *Damochlora spina*, Fig. 17.69I; *Glyptorhagada silveri*, Fig. 17.69K), and colour (*Rhagada harti*, Fig. 17.69H; *Cupedora sutilosa*, Fig. 17.69J; *Glyptorhagada silveri*, Fig. 17.69K and *Sinumelon bitaeniatum*, Fig. 17.69L).

Camaenids inhabit a wide variety of vegetation and climatic zones, from rainforest to near desert areas. Their diversity and abundance are greatest in semi-arid limestone areas, and reach a maximum in the Ningbing Ranges and Jeremiah Hills in the north-eastern corner of Western Australia. An endemic radiation of three genera has resulted in more than 28 mainly allopatric species (Solem 1988a), with total species ranges of 0.01–7.45 km² (median 0.825 km²). Few Australian camaenid species have extended geographic ranges.

Feeding includes breaking off bits of dead grass and leaves, taking bark from twigs, and scraping algal-fungal films off rocks, tree limbs, or living leaves. The specialised diets and feeding structures have evolved several times within the Camaenidae in different parts of Australia.

Many species are eaten by native and introduced rodents and possibly some native marsupials. Although bird and lizard predation is important in other regions of the world, we only have direct evidence that the Scrub Fowl (*Megapodius freycinet*) feeds on the camaenid *Amplirhagada castra* (Solem 1981b), on the Mitchell Plateau, Western Australia.

Few data are available on reproduction and life histories. Kimberley species, which live in an area with a predictable and dependable summer wet season that lasts four to seven months, are protandrous hermaphrodites with a maturation pattern characterised by several features (Solem & Christensen 1984). They reach half adult size in the wet season of birth. They complete shell growth and become male mature near the end of the second wet season, and are male active throughout the third wet season. They become female mature late in the third wet season, and are male and female active during fourth and successive wet seasons. They have a life span of at least eight, probably more than 10, years in all.

There are clear patterns of seasonality for adult organ size in the Kimberley taxa. Species from central Australia and the Flinders Ranges of South Australia also are protandrous hermaphrodites, but full sexual maturation precedes completion of shell growth, the length of life probably extends to 20 or more years, and size variation in adult organs is reduced because there is no dependable wet season. Taxa from the near desert regions show additional modifications in structure (Solem 1992, 1993). The one significant report on reproduction in the eastern Australian taxa (McLauchlan 1951) contains a number of significant observations and several hypotheses on mating, egg laying and life expectancy that need to be tested.

Aestivating snails may burrow into the sand or soil, lie loose in generally shaded litter or rock talus, or seal the shell aperture to a rock, piece of wood, or another snail shell. Those that seal to objects use a strengthened mucus, which may be so strong that the shell itself breaks first when an attempt is made to pull the shell loose. The calcified whole-aperture epiphragms are unusual in that gas exchange may take place around the edge of the epiphragm, rather than through a breathing pore (Solem 1986b).

A few wet area camaenids may become garden nuisances by feeding on ornamental plants, but otherwise they are not known to be of economic importance.

Camaenids are common and diverse from South-East Asia to Japan, the Philippines, Indonesia, and through New Guinea to the Solomon Islands. In the New World, they extend presently from the Greater Antilles and Costa Rica south to Bolivia. A moderate Cretaceous to Miocene fossil record in the United States (Solem 1978b) indicates a northern origin and a subsequent loss of northern range area. In Australia, camaenids apparently never reached, or were unable to colonise, either the humid south-western portion of Western Australia or Tasmania and the wetter parts of Victoria. The Kimberley and immediately adjacent areas of the Northern Territory have the largest camaenid fauna in Australia – about 185 species in 23 genera, of which 14 genera and all 185 species are endemics with restricted distributions. Very few Australian fossil camaenids are known, but Ludbrook (1978, 1984) and McMichael (1968) have published some records. Most published records are based upon incomplete casts that are difficult to interpret.

Superfamily HELICOIDEA

The helicoidean shell is small to very large (up to 100 mm in height), and usually helicoid in shape. However, the variations in shape are great and range from discoidal to turreted, rarely lenticular or often ovate-conic. The aperture is generally large and infrequently contains lamellae and denticles. Shell sculpture varies from smooth to strongly costulate, sometimes with additional periostracal elements. Shell colour ranges from drab brown to brightly coloured. The peristome is usually thickened and reflected. The form of the radula is variable but the basic pattern of weakly tricuspidate central teeth, bicuspidate lateral teeth and multicuspitate marginal teeth underlies a wide range of habitat-related modifications. The jaw may be smooth or ribbed (Pilsbry 1939).

The length of the kidney is variable and the ureter is sigmurethrous. The complex reproductive system includes dart sacs, accessory glands and other appendages. An epiphallus is present on the penis. Helicoideans are oviparous or ovoviviparous.

None of the three families included is native to Australia. However, two are represented by introduced species. The Helminthoglyptidae are a New World family widely distributed in North and South America and the West Indies. The Bradybaenidae are basically an Eurasian family, that includes some brightly coloured species from the Philippines. A widespread introduced species, *Bradybaena similis*, is present in Australia. The Helicidae are a western Palearctic group and include many species that have been spread widely by humans. A number of helcid species are now resident in Australia.

The Helicoidea includes the most advanced pulmonates and dates from the Cretaceous–Palaeocene of Europe and North America (Solem 1979a).

Family Helicidae

The Helicidae are a large family of terrestrial snails with globose, subglobose or conic shells. The family is native to the Palearctic Region of Europe, western Asia and North Africa but a number of species are accomplished world travellers (Smith 1989) and have become well established, and even dominant, in many temperate regions of the world. Eleven species have been introduced, mainly accidentally, into Australia with the European settlement of the continent (Smith 1992) and most have quickly become serious pests of gardens and crops. Petterd (1879b) recorded that *Helix aspersa* was introduced intentionally into Tasmania to provide food for introduced European birds such as the Thrush and Blackbird. These introductions have been documented by Musson (1890), Cotton (1954) and Smith & Kershaw (1979), and the extent of the problems caused by the introductions has been outlined by G.H. Baker (1986, 1988) and G.H. Baker & Vogelzang (1988).

The shells are dextral and vary in form from discoidal to subglobose, globose, and turreted to conic with an elevated spire (Fig. 17.71A–C). Shell size ranges from small to large (up to 60 mm in length). The shells are usually umbilicated and unicoloured but often with spiral bands or axial flammulations. The aperture is usually rounded, and lacks teeth or lamellae and the peristome is simple or reflected. The shell may be sculptured by growth lines, ripples, spiral striae and rugosities. The foot is fleshy and the sole is not discoidal.

Most helicids are herbivorous, feeding on living plants; a few feed on decaying plant material. The jaws are ribbed, plaited or costulate, rarely smooth, and the radula has many small, simple teeth in straight rows (Fig. 17.71E). The crop is large and the digestive tract is long. The length of the kidney varies from short to long and narrow in different groups.

Helicids are protandric hermaphrodites and usually have a dart sac and dart apparatus (Fig. 17.71D). The penis has a papilla or short verge and is continued into an epiphallus usually with a flagellum. Different subgroups vary in details of anatomical features of the reproductive system, such as the dart structures and the form of the spermatheca. Some groups are ovoviviparous but the majority lay hard-shelled eggs.

Helicids are the most widely studied group of land snails with regard to morphology, natural history, ecology and physiology (Baker, G.H. 1986). Some recent work has been done on the effects of Australian conditions on several species (Pomeroy & Laws 1967; Baker, G.H. 1986, 1988; Baker, G.H. & Vogelzang 1988). Mating occurs in early spring. Usually several clutches of white, hard-shelled eggs are laid in damp soil. Under favourable conditions of food and moisture, maturity can be reached in one year and breeding occurs. Some species seek shelter in cool, damp places where they secrete thick mucous epiphragms and aestivate over hot dry periods. Others, for example, *Cernuella* and *Theba* species, aestivate over the hot dry summers of South Australia and western Victoria above ground in very exposed places, such as on wooden posts (Fig. 17.71F; Smith 1981).

17. PULMONATA

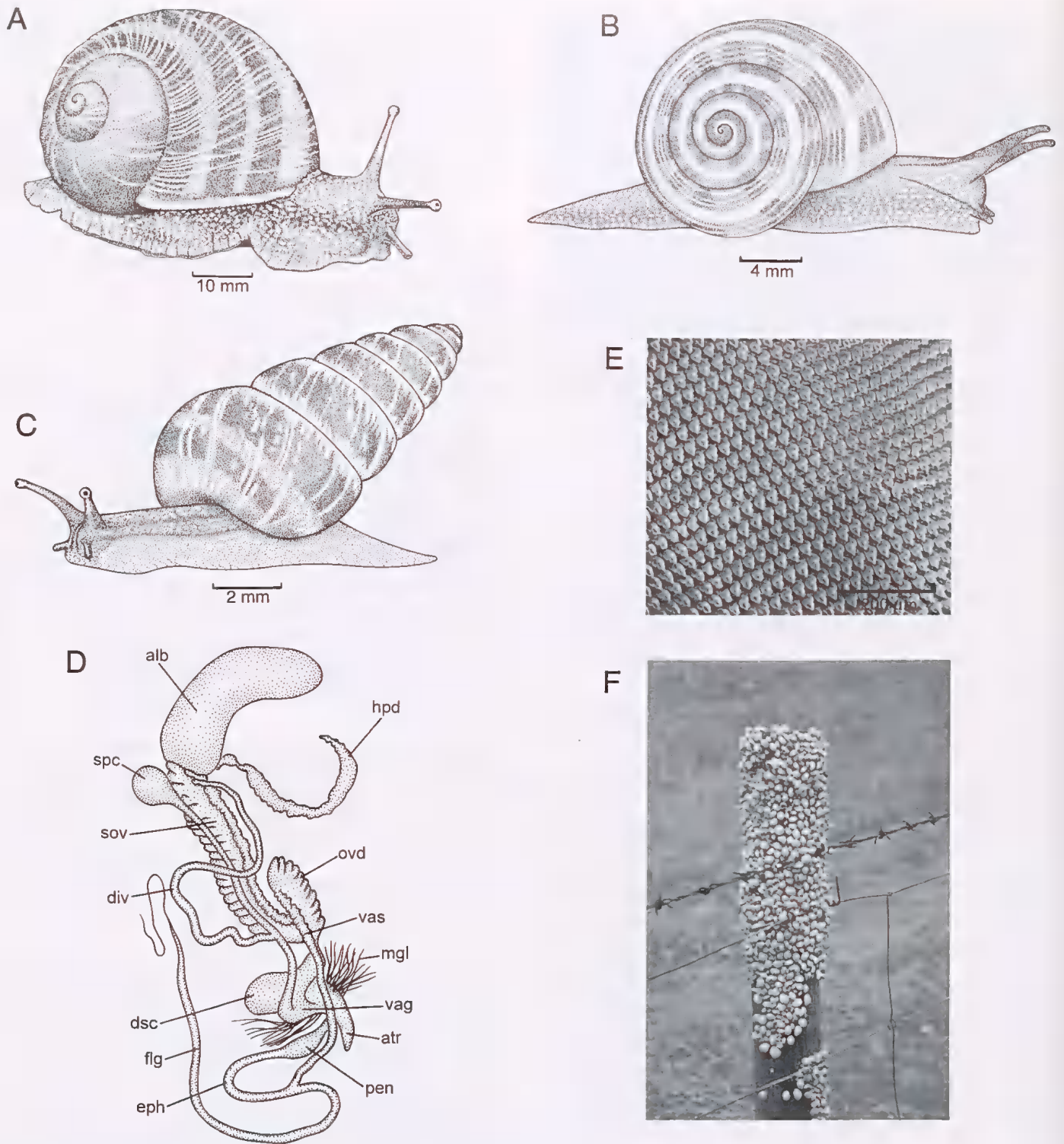


Figure 17.71 Family Helicidae. This family is represented in Australia by introduced species. A, *Helix aspersa*, a widespread garden pest. B, *Theba pisana* may attain high densities in the coastal sand-dunes of southern Australia. C, *Cochlicella barbara*. D, *Helix aspersa*, reproductive tract. E, *Helix aspersa*, portion of radula; F, *Theba pisana*, aestivating on a wooden fence post. alb, albumen gland; atr, atrium; div, diverticulum of spermathecal duct; dsc, dart sac; eph, epiphallus; flg, flagellum; hpd, hermaphroditic duct; mgl, mucous gland; ovd, oviduct; pen, penis; sov, spermoviduct; spc, spermatheca; vag, vagina; vas, vas deferens. (A, C, after photograph by B.J. Smith; B, drawn from live animals collected in Victoria; D, modified after Kerney & Cameron 1979)

[A–D, C. Eadie; E, B.J. Smith; F, G. Baker]

Helix aspersa, *Theba pisana* and species of *Cochlicella* and *Cernuella* are considered pests of gardens, pasture, orchards and stored crops in many parts of southern and eastern Australia (Smith 1981; Baker, G.H. 1986). They are confined mostly to the modified environments of southern Australia, particularly where watering and the cultivation of introduced plants provide favourable conditions, though *Theba pisana* is also found in semi-arid areas such as coastal dunes (Smith 1967b). They are not associated with any animal or human health problems. *Helix pomatia* and *H. aspersa* are widely used for human consumption in Europe, particularly France and Spain. Imported canned *H. pomatia* is available in Australia, and live snails are

occasionally seized by Quarantine Officers at international airports while being smuggled in as food and/or breeding stock. *Helix aspersa* is bred commercially for the table in several parts of southern Australia.

Following H.B. Baker (1956), Burch (1976b) suggested that the Australian species in the group treated here as the family Helicidae should in fact be separated into two families, the Helicidae and the Hygromiidae or Helicellidae. However, they are here treated as subfamilies of the one family, Helicidae, following Zilch (1959) and others. This is one of the largest of land snail families with over 300 named genera (Zilch 1959).

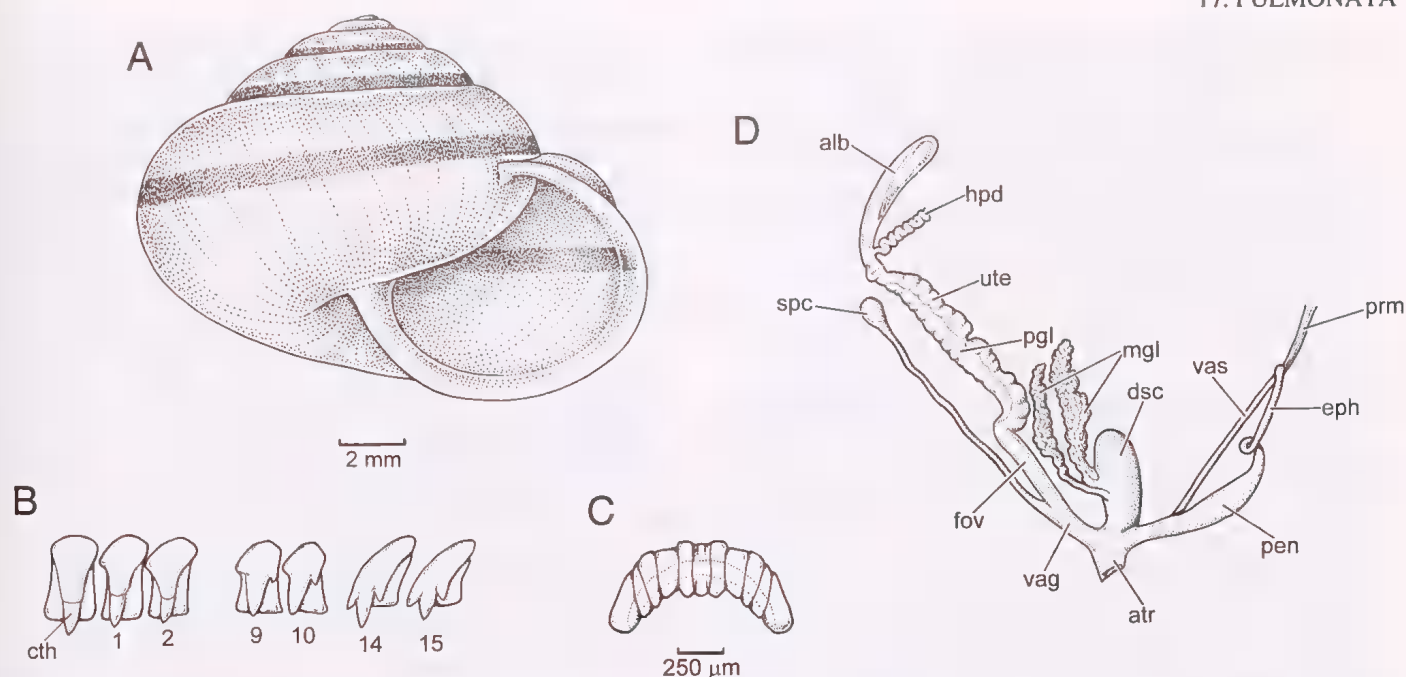


Figure 17.72 Family Bradybaenidae. Introduced from China, *Bradybaena similaris* is the only bradybaenid species known to occur in Australia. A, shell, apertural view of banded form; B, some radular teeth from half of one transverse row, numbers denote position of teeth from the central tooth; C, jaw; D, reproductive tract. alb, albumen gland; atr, atrium; cth, central tooth; dsc, dart sac; eph, epiphallus; fov, free oviduct; hpd, hermaphroditic duct; mgl, mucous gland; pen, penis; pgl, prostate gland; prm, penial retractor muscle; spc, spermatheca; ute, uterus; vag, vagina; vas, vas deferens. (B, C, after Benthem Jutting 1950; D, after Pilsbry 1894)

Family Bradybaenidae

The Bradybaenidae include arboreal and terrestrial land snails with small to large shells which vary in shape from depressed to helicoid or globose-conic (Figs 17.22A, 17.72A). In some groups the shells are smooth and polished, or strongly sculptured and sometimes covered with a hairy periostracum. Shell colour is variable. The family includes a number of very colourful species from the Philippines. Species from Europe and Asia are less spectacularly coloured.

A single introduced species, *Bradybaena similaris*, occurs in Australia. It is endemic in eastern Asia, from southern China to Java and Sulawesi, but elsewhere has been widely distributed by commerce (Benthem Jutting 1950; Solem 1959b).

The jaw is strongly ribbed (Fig. 17.72C) and the radula usually has tricuspidate central and lateral teeth in which the accessory cusps may be secondarily reduced (Fig. 17.72B). The marginal teeth are multicuspidate. The reproductive system usually has a dart sac and dart apparatus (Pilsbry 1894). When present, mucous glands are sacculate and arise from the base of the dart sac. The penis usually has an accompanying epiphallus and flagellum (Fig. 17.72D).

Two subfamilies are recognised: the Helicostylinae which includes the larger, colourful tree snails of the Philippines region; and the largely terrestrial Bradybaeninae, which occur through Asia, China, Japan and parts of eastern Africa.

Bradybaena similaris is polymorphic in shell colour; a circum-peripheral red band may or may not be present (Fig. 17.72A). The shell may be yellow or brown. Komai & Emura (1955) investigated the genetic basis of this polymorphism but could find no correlation between polymorphism frequencies and environmental factors, including predation by birds.

Bradybaena similaris is a known agricultural pest in eastern Australia (Godan 1983) and needs to be monitored. The snail is able to increase to large population densities and in parts of southern Queensland it has become a nuisance pest in cucurbit crops. The sheer numbers of adult and juvenile snails, and their faecal deposits, interfere with the 'clean' harvesting of produce.

The species is established in coastal areas from southern New South Wales to the Cairns region of northern Queensland where it has been recorded from the Atherton Tableland. Benthem Jutting (1950) provided a useful synopsis of its non-Australian distribution.

LITERATURE CITED

- Allan, J. (1950). *Australian Shells: with related animals living in the sea, in freshwater and on the land*. Georgian House : Melbourne xix 470 pp.
- Altena, C.O. van R. & Smith, B.J. (1975). Notes on introduced slugs of the families Limacidae and Milacidae in Australia, with two new records. *Journal of the Malacological Society of Australia* 3: 63–80
- Andrews, E.B. (1988). Excretory systems of molluscs. Pp. 381–448 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca*. Vol. 11. *Form and function*. Academic Press : New York
- Awati, P.R. & Karandikar, K.R. (1948). *Oncidium verruculatum*, Cuv. (Anatomy, Embryology and Bionomics). *Zoological Memoirs of the University of Bombay* No. 1 52 pp.
- Baker, F.C. (1945). *The Molluscan Family Planorbidae*, with memorial by H.J. van Cleave. University of Illinois Press : Urbana xxxvi 530 pp.
- Baker, G.H. (1986). The biology and control of white snails (Mollusca: Helicidae), introduced pests in Australia. *CSIRO Australia, Division of Entomology, Technical Paper* No. 25: 1–31
- Baker, G.H. (1988). The life history, population dynamics and polymorphism of *Cernuella virgata* (Mollusca: Helicidae). *Australian Journal of Zoology* 36: 497–512
- Baker, G.H. & Vogelzang, B.K. (1988). Life history, population dynamics and polymorphism of *Theba pisana* (Mollusca: Helicidae) in Australia. *Journal of Applied Ecology* 25: 867–887

17. PULMONATA

- Baker, H.B. (1925). Nomenclature of Veronicellidae (Vaginulidae). *The Nautilus* 39: 13–18
- Baker, H.B. (1941). Zonitid snails from Pacific islands. Parts 3 and 4. 3, genera other than Microcystinae [pp. 203–346]; 4, distribution and indexes [pp. 347–370]. *Bulletin of the Bernice P. Bishop Museum* 166: 203–370
- Baker, H.B. (1955). Heterurethrous and aulacopod. *The Nautilus* 68: 109–112
- Baker, H.B. (1956). Family names in Pulmonata. *The Nautilus* 69: 128–139
- Baker, H.B. (1962). Puerto Rican Holopodops. *The Nautilus* 75: 116–121
- Bargmann, H.E. (1930). The morphology of the central nervous system in the Gastropoda Pulmonata. *Journal of the Linnean Society of London (Zoology)* 37: 1–59
- Bartsch, P. & Quick, M.E. (1926). An anatomic study of *Zonitoides arboreus* Say. *Journal of Agricultural Research (Washington D.C.)* 32(8): 783–791
- Baur, B. & Chen, X. (1993). Genital dimorphism in the land snail *Chondrina avenacea*: frequency of aphyall in natural populations and morph-specific allocation to reproductive organs. *The Veliger* 36: 252–258
- Bayne, C.J. (1973). Physiology of the pulmonate reproductive tract: location of spermatozoa in isolated, self-fertilising succinid snails (with a discussion of pulmonate tract terminology). *The Veliger* 16: 169–175
- Bentham Jutting, W.S.S. van (1950). Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. II. Critical revision of the Javanese pulmonate land-shells of the families Helicarionidae, Pleurodontidae, Fruticicolidae and Streptaxidae. *Treubia* 20: 381–505
- Bentham Jutting, W.S.S. van (1951). On the anatomy of *Achatina fulica* (Férussac). *Treubia* 21: 111–113
- Bentham Jutting, W.S.S. van (1952). Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. III. Critical revision of the Javanese pulmonate land-snails of the families Ellobiidae to Limacidae, with an appendix on Helicarionidae. *Treubia* 21: 291–435
- Bentham Jutting, W.S.S. van (1954). The Malayan Streptaxidae of the genera *Discartemon* and *Oophana*. *Bulletin of the Raffles Museum* 25: 71–106
- Bentham Jutting, W.S.S. van (1956). Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago. V. Critical revision of the Javanese freshwater gastropods. *Treubia* 23: 259–477
- Bentham Jutting, W.S.S. van (1963). Non-marine Mollusca of West New Guinea. Part 1. Mollusca from fresh and brackish waters. *Nova Guinea* 20: 409–521
- Bentham Jutting, W.S.S. van (1964). Non-marine Mollusca of West New Guinea, Part 3, Pulmonata, I. *Nova Guinea, Zoology* 32: 205–304
- Bieler, R. (1992). Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics* 23: 311–338
- Binney, G.W. (1878). The terrestrial air-breathing mollusks of the United States and the adjacent territories of North America, Vol. 5. *Bulletin of the Museum of Comparative Zoology* 1: 1–449
- Bishop, M.J. (1977). Terrestrial Mollusca of Queensland. The family Veronicellidae. *Memoirs of the Queensland Museum* 18: 53–59
- Bishop, M.J. (1978). *Zonitoides arboreus* (Say) (Pulmonata: Zonitidae) introduced into Australia and the identity of *Alienator* Iredale. *Journal of the Malacological Society of Australia* 4: 7–8
- Bishop, M.J. (1981). The biogeography and evolution of Australian land snails. Pp. 925–954 in Keast, A. (ed.) *Ecological Biogeography of Australia. Monographiae Biologiae* 41. W. Junk: The Hague
- Blair, D. & Islam, K.S. (1983). The life cycle and morphology of *Trichobilharzia australis* n.sp. (Digenea: Schistosomatidae) from the nasal blood vessels of the black duck (*Anas superciliosa*) in Australia, with a review of the genus *Trichobilharzia*. *Systematic Parasitology* 5: 89–117
- Boer, H.H., Slot, J.J.W. & Van Anel, J. (1968). Electron microscopical and histochemical observations on the relation between medio-dorsal bodies and neurosecretory cells in the basommatophoran snails *Lymnaea stagnalis*, *Ancylus fluviatilis*, *Australorbis glabratus* and *Planorbis corneus*. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* 87: 435–450
- Boray, J.C. (1964). Studies on the ecology of *Lymnaea tomentosa*, the intermediate host of *Fasciola hepatica*. I. History, geographical distribution, and environment. *Australian Journal of Zoology* 12: 217–230
- Boray, J.C. (1969). Experimental fasciolosis in Australia. Pp. 95–210 in Dawes, B. (ed.) *Advances in Parasitology*. Vol. 7. Academic Press: New York
- Boray, J.C. & McMichael, D.F. (1961). The identity of the Australian lymnaeid snail host of *Fasciola hepatica* L. and its response to environment. *Australian Journal of Marine and Freshwater Research* 12: 150–163
- Boss, K.J. (1982). Mollusca. Pp. 945–1166 in Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms*. Vol. 1. McGraw-Hill Book Company: New York
- Brettnall, B.W. (1919). Onchidiidae from Australia and the South-Western Pacific Islands. *Records of the Australian Museum* 12: 303–328
- Breure, A.S.H. (1978). Notes on and descriptions of Bulimulidae (Mollusca, Gastropoda). *Zoologische Verhandelingen* 164: 1–255
- Breure, A.S.H. (1979). Systematics, phylogeny and zoogeography of Bulimulinae (Mollusca). *Zoologische Verhandelingen* 168: 1–215
- Breure, A.S.H. & Eskens, A.A.C. (1981). Notes on and descriptions of Bulimulidae (Mollusca, Gastropoda), II. *Zoologische Verhandelingen* 186: 1–111
- Breure, A.S.H. & Schouten, J.R. (1985). Notes on and descriptions of Bulimulidae (Mollusca, Gastropoda), III. *Zoologische Verhandelingen* 216: 1–98
- Britton, K.M. (1984). The Onchidiacea (Gastropoda, Pulmonata) of Hong Kong with a worldwide review of the genera. *Journal of Molluscan Studies* 50: 179–191
- Brown, D.S. (1981). Observations on Planorbinae from Australia and New Guinea. *Journal of the Malacological Society of Australia* 5: 67–80
- Bruggen, A.C. van (1967). An introduction to the pulmonate family Streptaxidae. *Journal of Conchology* 26: 181–188
- Bruggen, A.C. van (1980). Gondwanaland connections in the terrestrial molluscs of Africa and Australia. *Journal of the Malacological Society of Australia* 4: 215–222
- Bunn, S.E. & Stoddart, J.A. (1983). A new species of the prosobranch gastropod *Glacidorbis* and its implications for the biogeography of South-Western Australia. *Records of the Western Australian Museum* 11: 49–57
- Burch, J.B. (1962). *How to Know the Eastern Land Snails*. W.C. Brown Co.: Dubuque, Iowa 214 pp.
- Burch, J.B. (1968). Tentacle retraction in Tracheopulmonata. *Journal of the Malacological Society of Australia* 1(11): 62–67
- Burch, J.B. (1976a). Snails without shells. *Australian Natural History* 18: 310–315
- Burch, J.B. (1976b). Outline of classification of Australian terrestrial molluscs (native and introduced). *Journal of the Malacological Society of Australia* 3: 127–156
- Burch, J.B. (1976c). Mollusca. Pp. 109–124 in Broadbent, J. & Clark, S. (eds) *A Faunal Survey of East Australian Rainforests, Interim Report*. Australian Museum: Sydney
- Burch, J.B. & Lindsay, G.K. (1973). Taxonomic groupings in the Lymnaeidae. *Bulletin of the American Malacological Union* 38: 15
- Burch, J.B. & Patterson, C.M. (1969). The systematic position of the Athoracophoridae (Gastropoda: Euthyneura). Pp. 259–260 in Paget, O.E. (ed.) *Proceedings of the Third European Malacological Congress, Vienna, 4–6 September 1968*. Malacologia 9
- Burch, J.B. & Patterson, C.M. (1971a). Chromosome numbers of Hawaiian Lymnaeidae. *Malacological Review* 4: 209–210

- Burch, J.B. & Patterson, C.M. (1971b). The chromosome number of the athoracophorid slug, *Triboniophorus graeffei*, from Australia. *Malacological Review* 4: 25–26
- Burch, J.B. & Tottenham, J.L. (1980). North American freshwater snails. *Transactions of the POETS Society* 3: 81–215
- Burton, D.W. (1980). Anatomical studies on Australian, New Zealand and subantarctic Athoracophoridae (Gastropoda: Pulmonata). *New Zealand Journal of Zoology* 7: 173–198
- Carriker, M.R. (1946). Morphology of the alimentary system of the snail *Lymnaea stagnalis* Say. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 38: 1–88
- Chalmer, P.N. & Kendrick, G.W. (1975). A molluscan intermediate host to *Fasciola hepatica* Linnaeus feral in south-western Australia. *Western Australian Naturalist* 13(4): 87–88
- Climo, F.M. (1969). Classification of New Zealand Arionacea (Mollusca: Pulmonata) II. Revision of *Charopa* subgenus *Ptychodon* Ancey, 1888. *Records of the Dominion Museum* 6: 175–258
- Climo, F.M. (1970). Classification of New Zealand Arionacea (Mollusca: Pulmonata) III. A revision of the genera *Charopa* Albers, 1860 (excluding subgenus *Ptychodon* Ancey, 1888), *Phenacharopa* Pilsbry, 1893 and *Flammocharopa* n. gen. Endodontidae: Endodontinae. *Records of the Dominion Museum* 6: 285–366
- Climo, F.M. (1977). A new higher classification of New Zealand Rhytididae (Mollusca: Pulmonata). *Journal of the Royal Society of New Zealand* 7: 59–65
- Climo, F.M. (1978). Classification of New Zealand Arionacea (Mollusca: Pulmonata) A revision of the New Zealand charopine snails with lamellate apertures. *Records of the National Museum of New Zealand* 1(12): 177–201
- Climo, F.M. (1980). Smeagolida, a new order of gymnomorph molluscs from New Zealand based on a new genus and species. *New Zealand Journal of Zoology* 5: 275–288
- Colman, P.H. (1977). An introduction of *Achatina fulica* to Australia. *Malacological Review* 10: 77–78
- Colman, P.H. (1987). Blazing snail trails. *Australian Natural History* 22: 119
- Colman, P.H. & Burch, J.B. (1977). Molluscs. Pp. 54–58 in Goldstein, W. (ed.) *Rainforests*. Reprinted from *Parks and Wildlife* 2(1). National Parks and Wildlife Service: Hurstville, New South Wales
- Comery, J. & Ward, G. (1985). Slugs in field crops and pastures. Agnote 130/622, Department of Agriculture, Victoria 2 pp.
- Cooke, C.M. & Kondo, Y. (1960). Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). *Bulletin of the Bernice P. Bishop Museum* 221: 1–303
- Cotton, B.C. (1954). A catalogue of introduced snails and slugs in Australia. *Records of the South Australian Museum* 11: 177–187
- Cox, J.C. (1864). *Catalogue of Specimens of the Australian Land Shells in the Collection of James C. Cox*. John Alex Engel: Sydney 44 pp.
- Cox, J.C. (1868). *A Monograph of Australian Land Shells*. William Maddock: Sydney 110 pp.
- Crampton, H.E. (1916). Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. *Carnegie Institute of Washington Publication* 228: 1–311
- Crampton, H.E. (1925). Studies on the variation, distribution, and evolution of the genus *Partula*. The species of the Mariana Islands, Guam and Saipan. *Carnegie Institute of Washington Publication* 228a: 1–116
- Crampton, H.E. (1932). Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Moorea. *Carnegie Institute of Washington Publication* 410: 1–335
- Creese, R.G. (1980). Reproductive cycles and fecundities of two species of *Siphonaria* (Mollusca, Pulmonata) in south-eastern Australia. *Australian Journal of Marine and Freshwater Research* 31: 33–47
- Dakin, W.J. (1947). The true sea-slug – *Onchidium*. *Australian Museum Magazine* 9: 141–144
- Dakin, W.J. (1952). *Australian Seashores. A guide for the beach-lover, the naturalist, the shore fisherman, and the student*. Angus & Robertson: Sydney xii 372 pp.
- Dale, B. (1973). Blood pressure and its hydraulic functions in *Helix pomatia* L. *Journal of Experimental Biology* 59: 477–490
- Dale, B. (1974). Extrusion, retraction and respiratory movements in *Helix pomatia* in relation to distribution and circulation of the blood. *Journal of Zoology, London* 173: 427–439
- Dance, S.P. (1986). *A History of Shell Collecting*. Leiden: E.J. Brill & W. Backhuys xv 265 pp.
- Daniell, A. (1991). Taxonomy, genetics and ecology of the terrestrial slug family Cystopeltidae (Mollusca: Pulmonata). Unpubl. Ph.D. thesis, School of Biological Sciences, Latrobe University, Victoria
- Daniell, A. (1994). Genetics and terrestrial mollusc conservation. *Memoirs of the Queensland Museum* 36: 47–53
- Dartnall, A.J. & Dartnall, J.A. (1972). Notes on the reproductive anatomy and cytogenetics of some Australian acavacean molluscs. *Australian Journal of Zoology* 20: 79–81
- Dartnall, A.J. & Kershaw, R.C. (1978). Description of a new species of *Helicarion* (Stylommatophora: Helicarionidae) in Tasmania. *Records of the Queen Victoria Museum* 62: 1–18
- Davies, O.B. (1912). The anatomy of the slug, *Cystopelta petterdi* var. *purpurea* var. nov. *Proceedings of the Royal Society of Victoria* 24: 331–342
- Davies, O.B. (1914). The anatomy of *Caryodes dufresnii* Leach. *Proceedings of the Royal Society of Victoria* 27: 19–24
- De Wilde, J.J.A. (1984). The anatomy of an *Atopos*-species from Papua New Guinea with a discussion on its systematic position (Mollusca, Gastropoda, Rathouisiidae). *Indo-Malayan Zoology* 1: 113–126
- Delhay, W. & Bouillon, J. (1972a). L'évolution et l'adaptation de l'organe excréteur chez les mollusques gastéropodes pulmonés. I. Introduction générale et histophysiologie comparée du rein chez les Basommatophores. *Bulletin Biologique de la France et de la Belgique* 106: 45–77
- Delhay, W. & Bouillon, J. (1972b). L'évolution et l'adaptation de l'organe excréteur chez les mollusques gastéropodes pulmonés. II. Histophysiologie comparée du rein chez les Stylommatophores. *Bulletin Biologique de la France et de la Belgique* 106: 123–142
- Delhay, W. & Bouillon, J. (1972c). L'évolution et l'adaptation de l'organe excréteur chez les mollusques gastéropodes pulmonés. III. Histophysiologie comparée du rein chez les Soléolifères et conclusions générales pour tous les pulmonés. *Bulletin Biologique de la France et de la Belgique* 106: 295–314
- Duncan, C.J. (1958). The anatomy and physiology of the reproductive system of the freshwater snail *Physa fontinalis* (L.). *Proceedings of the Zoological Society of London* 131: 55–85
- Duncan, C.J. (1960). The evolution of the pulmonate genital system. *Proceedings of the Zoological Society of London* 134: 601–609
- Duncan, C.J. (1975). Reproduction. Pp. 309–365 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. Academic Press: London
- Dundee, D.S. & Baerwald, R.J. (1984). Observations on a micropredator, *Gulella bicolor* (Hutton) (Gastropoda: Pulmonata: Streptaxidae). *The Nautilus* 98: 63–68
- Emberton, K.C. (1988). The genitalic, allozymic, and conchological evolution of the eastern North American Triodopsinae (Gastropoda: Pulmonata: Polygyridae). *Malacologia* 28: 159–273
- Emberton, K.C. (1989). Retraction/extension and measurement error in a land snail: effects on systematic characters. *Malacologia* 31: 157–173
- Emberton, K.C. (1991). Polygyrid relations: a phylogenetic analysis of 17 subfamilies of land snails (Mollusca: Gastropoda: Stylommatophora). *Zoological Journal of the Linnean Society* 103: 207–224

- Emberton, K.C., Kuncio, G.S., Davis, G.M., Phillips, S.M., Monderewicz, K.M. & Yan Hua Guo (1990). Comparison of recent classifications of stylommatophoran land-snail families, and evaluation of large-ribosomal-RNA sequencing for their phylogenetics. *Malacologia* 31: 327–352
- Evans, W.A.L. & Jones, E.G. (1962). Carbohydrases in the alimentary tract of the slug *Arion ater* L. *Comparative Biochemistry and Physiology* 5: 149–160
- Featherston, D.W., Weeks, P.J. & Featherston, N. (1988). Schistosome dermatitis in Lake Wanaka: *Cercaria longicauda* prevalence in *Lymnaea tomentosa* 1978–83. *New Zealand Journal of Zoology* 15: 381–386
- Fischer, P.H. (1883). Sur le genre *Coelioxys*. *Journal of Conchyliologie* 31: 98–102
- Fischer, P.H. (1887). *Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles*, suivi d'un appendice sur les Brachiopodes par D.P. Cœhlert. F. Savy : Paris 1369 pp., 1138 figs, 23 pls
- Forbes, E. (1851). On the Mollusca collected by Mr MacGillivray during the voyage of the *Rattlesnake*. Pp. 360–386 in MacGillivray, J. Narrative of the voyage of H.M.S. *Rattlesnake* ... during ... 1846–1850. Including discoveries and surveys in New Guinea, the Louisiade Archipelago, etc. To which is added the account of Mr. E.B. Kennedy's expedition for the exploration of the Cape York Peninsula [including Mr. W. Carron's narrative]. London 2 vols
- Forcart, L. (1969). Veronicellid land slugs from the New Hebrides, with description of *Semperula solemi* new species. *Fieldiana Zoology* 51: 147–156
- Fraser, L.A. (1946). The embryology of the reproductive tract of *Lymnaea stagnalis appressa* Say. *Transactions of the American Microscopical Society* 65: 279–298
- Fretter, V. (1943). Studies in the functional morphology and embryology of *Onchidella celtica* (Forbes & Hanley) and their bearing on its relationships. *Journal of the Marine Biological Association of the United Kingdom* 25: 685–720
- Fretter, V. (1975). Introduction. Pp. xi–xxix in Fretter, V. & Peake, J.F. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. London : Academic Press
- Geraerts, W.P.M. & Joosse, J. (1984). Freshwater snails (Basommatophora). Pp. 141–207 in Tompa, A.S., Verdonk, N.H. & Van den Biggelaar, J.A.M. (eds) *The Mollusca. Vol. 7. Reproduction*. Academic Press : New York
- Ghiretti, F. & Ghiretti-Magaldi, A. (1975). Respiration. Pp. 33–52 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. Academic Press : London
- Ghose, K.C. (1963). The alimentary system of *Achatina fulica*. *Transactions of the American Microscopical Society* 82: 149–167
- Gittenberger, E. (1973). Beiträge zur Kenntnis der Pupillacea. III Chondrininae. *Zoologische Verhandlungen* 127: 1–267
- Giusti, F., Manganelli, G. & Selmi, G. (1991). Spermatozoon fine structure in the phylogenetic study of the Helicoidea (Gastropoda, Pulmonata). *Proceedings of the Tenth Malacological Congress (Tübingen, 1989)* pp. 611–616
- Godan, D. (1983). *Pest Slugs and Snails. Biology and Control*. Springer-Verlag : Berlin 445 pp.
- Goodfriend, G.A. (1986). Radiation of the land snail genus *Sagda* (Pulmonata: Sagdidae): comparative morphology, biogeography and ecology of the species of north-central Jamaica. *Zoological Journal of the Linnean Society* 87: 367–398
- Griffond, B., Dadkhah-Teherani, Z., Medina, A. & Bride, M. (1991). Ultrastructure of *Helix aspersa* spermatogenesis: scanning and transmission electron microscopical contributions. *Journal of Molluscan Studies* 57: 277–287
- Grimpe, G. & Hoffman, H. (1925a). Versuch einer revision der indischen, indo-und polynesischen Vaginuliden (Gastropoden Pulmonata). *Zeitschrift für Wissenschaftliche Zoologie* 124: 1–50
- Grimpe, G. & Hoffman, H. (1925b). Die Nacktschnecken von Neu-Caledonien, den Loyalty Inseln und Neuen Hebriden. *Nova Caledonia, Zoology* 3: 339–476
- Harris, G.F. (1897). *Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History). Part I. The Australasian Tertiary Mollusca*. British Museum (Natural History) : London 407 pp. 8 pls
- Haszprunar, G. (1985). The Heterobranchia – a new concept of the phylogeny of the higher Gastropoda. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 23: 15–37
- Haszprunar, G. (1988). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies* 54: 367–441
- Haszprunar, G. & Huber, G. (1990). On the central nervous system of Smeagolidae and Rhodopidae, two families questionably allied with the Gymnomorpha (Gastropoda: Euthyneura). *Journal of Zoology, London* 220: 185–199
- Haven, N. (1973). Reproduction, development and feeding of the Australian marine pulmonate, *Trimusculus (Gadinia) conica*. *The Veliger* 16: 61–65
- Healy, J.M. (1983). An ultrastructural study of basommatophoran spermatozoa (Mollusca: Gastropoda). *Zoological Scripta* 12: 57–66
- Healy, J.M. (1986). Electron microscopic observations on the spermatozoa of a marine 'pulmonate' slug, *Onchidium damellii* (Gastropoda, Onchidiacea). *Journal of Submicroscopical Cytology* 18: 587–594
- Healy, J.M. (1988a). Sperm morphology and its systematic importance in the Gastropoda. Pp. 251–266 in Ponder, W.F. (ed.) *Prosobranch Phylogeny*. *Malacological Review, Supplement 4*
- Healy, J.M. (1988b). The ultrastructure of spermatozoa and spermiogenesis in pyramidellid gastropods, and its systematic importance. *Helgoländer Meeresuntersuchungen* 42: 303–318
- Healy, J.M. (1993). Comparative sperm ultrastructure and spermiogenesis in basal heterobranch gastropods (Valvatoidea, Architectonicoidea, Rissoelloidea, Omalogyroidea, Pyramidelloidea) (Mollusca). *Zoologica Scripta* 22: 263–276
- Healy, J.M. (1996). Molluscan sperm ultrastructure: correlation with taxonomic units within the Gastropoda, Cephalopoda and Bivalvia. Pp. 99–113 in Taylor, J. (ed.) *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press : London
- Healy, J.M. & Jamieson, B.G.M. (1989). An ultrastructural study of spermatozoa of *Helix aspersa* and *Helix pomatia* (Gastropoda, Pulmonata). *Journal of Molluscan Studies* 55: 389–404
- Hedley, C. (1889a). Anatomical notes on the Helicidae. Part III. *Proceedings of the Royal Society of Queensland* 6: 249–251
- Hedley, C. (1889b). On *Aneitea graeffei* and its allies. *Proceedings of the Royal Society of Queensland* 5: 162–173
- Hedley, C. (1890). On the structure and systematic position of *Cystopelta*. *Proceedings of the Linnean Society of New South Wales* (2) 5: 44–46
- Hedley, C. (1892). On the genus *Perrieria*. *Proceedings of the Linnean Society of New South Wales. Second series* 7: 311–313
- Hedley, C. (1893). On *Parmacochlea fischeri* Smith. *The Macleay Memorial Volume, Linnean Society of New South Wales*: 201–204
- Hedley, C. (1924). Some notes on Australian land shells. *Australian Zoologist* 3: 215–222
- Hesse, P. (1933). Zur anatomie und Systematik der Familie Enidae. *Archiv für Naturgeschichte N.F.* 2: 145–224
- Hill, D.H., Playford, G. & Woods, J.T. (eds) (1970). *Cainozoic Fossils of Queensland*. Queensland Palaeontographical Society : Brisbane 36 pp.
- Hoagland, K.E. & Davis, G.M. (1987). The succineid snail fauna of Chittenaugo Falls, New York: taxonomic status with comparisons to other relevant taxa. *Proceedings of the Academy of Natural Sciences of Philadelphia* 139: 465–526
- Hoffman, H. (1928). Zur Kenntnis der Onchidiiden (Gastrop. Pulmon). Ein Beitrag zur geographischen Systematik dieser Familie. I Untersuchung neuen materials und revision der Familie. *Zoologische Jahrbücher, Abteilung Systematik* 55: 29–118

- Hoffman, H. (1929). Zur Kenntnis der Onchidiiden (Gastrop. Pulmon). Ein Beitrag zur geographischen Verbreitung, Phylogenie und Systematik dieser Familie. II Phylogenie und Verbreitung. *Zoologische Jahrbücher, Abteilung Systematik* 57: 253–302
- Hubendick, B. (1945a). On the family Amphibolidae. *Proceedings of the Malacological Society of London* 26: 103–110
- Hubendick, B. (1945b). Phylogenie und Tiergeographie der Siphonariidae zur Kenntnis der Phylogenie in der Ordnung Basommatophora und des Ursprungs der Pulmonatengruppe. *Zoologiska Bidrag från Uppsala* 24: 1–126
- Hubendick, B. (1946). Systematic monograph of the Patelliformia. *Kungliga Svenska Vetenskapsakademiens Handlingar, Series 3* 23: 1–93
- Hubendick, B. (1948). Studies on *Bulinus*. *Arkiv för Zoologi* 40A(16): 1–63 f050703?
- Hubendick, B. (1951). Recent Lymnaeidae: Their variation, morphology, taxonomy, nomenclature and distribution. *Kungliga Svenska Vetenskapsakademiens Handlingar* 3(1): 1–223
- Hubendick, B. (1954). On a small quantity of *Siphonaria* material from Queensland. *Memoirs of the National Museum of Victoria* 19: 126–136
- Hubendick, B. (1955). Phylogeny in the Planorbidae. *Transactions of the Zoological Society of London* 28: 453–542
- Hubendick, B. (1956). A conchological survey of the genus *Plecotrema* (Gastropoda, Ellobiidae). *Proceedings of the Malacological Society of London* 32: 110–126
- Hubendick, B. (1957). The eating function in *Lymnaea stagnalis* (L.). *Arkiv för Zoologi* 10: 511–521
- Hubendick, B. (1960). A note on "*Pettancylus*" *australicus* (Tate). *Journal of the Malacological Society of Australia* 1(4): 32–38
- Hubendick, B. (1967). Studies on Ancyliidae. The Australia, Pacific and Neotropical formgroups. *Göteborgs Kungliga Vetenskaps och Vitterhets Samhälles Handlingar, Zoologica* 1: 5–52
- Hubendick, B. (1978). Systematics and comparative morphology of the Basommatophora. Pp. 1–47 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 2A. Systematics, evolution and ecology*. Academic Press: London
- Hyman, L. (1967). *The Invertebrates: Vol. VI Mollusca I*. McGraw-Hill: New York vii 792 pp.
- Inaba, A. (1969). Cytotaxonomic studies of lymnaeid snails. *Malacologia* 7: 143–168
- Iredale, T. (1926). Three Victorian species of *Ophicardelus* (Class Mollusca). *Victorian Naturalist* 42: 268–270
- Iredale, T. (1930). Notes on some desert snails. *Victorian Naturalist* 47: 118–20
- Iredale, T. (1933). Systematic notes on Australian land shells. *Records of the Australian Museum* 19: 37–59
- Iredale, T. (1937a). A basic list of the land Mollusca of Australia. *Australian Zoologist* 8: 287–333
- Iredale, T. (1937b). A basic list of the land Mollusca of Australia. – Part II. *Australian Zoologist* 9: 1–39
- Iredale, T. (1937c). An annotated check list of the land shells of South and Central Australia. *South Australian Naturalist* 18: 6–57
- Iredale, T. (1938). A basic list of land Mollusca of Australia. – Part III. *Australian Zoologist* 9: 83–124
- Iredale, T. (1939). A review of the land Mollusca of Western Australia. *Journal of the Royal Society of Western Australia* 25: 1–88
- Iredale, T. (1940a). Marine molluscs from Lord Howe Island, Norfolk Island, Australia and New Caledonia. *Australian Zoologist* 9: 429–443
- Iredale, T. (1940b). Guide to the land shells of New South Wales. *Australian Naturalist* 10: 227–236
- Iredale, T. (1941). Guide to the land shells of New South Wales. *Australian Naturalist* 10: 262–269
- Iredale, T. (1943a). A basic list of the freshwater Mollusca of Australia. *Australian Zoologist* 10: 188–230
- Iredale, T. (1943b). Guide to the freshwater shells of New South Wales, Part I. *Australian Naturalist* 11: 85–95
- Iredale, T. (1943c). Guide to the land shells of New South Wales. Part 5. *Australian Naturalist* 11: 61–69
- Iredale, T. (1944a). The land Mollusca of Lord Howe Island. *Australian Zoologist* 10: 299–334
- Iredale, T. (1944b). Guide to the freshwater shells of New South Wales, Part II. *Australian Naturalist* 11: 113–127 f050704
- Iredale, T. (1945). The land Mollusca of Norfolk Island. *Australian Zoologist* 11: 46–71
- Jenkins, B.W. (1981). *Siphonaria funiculata* Reeve (Siphonariidae, Pulmonata): a redescription making *S. virgulata* Hedley a geographical variant of *S. funiculata*. *Journal of the Malacological Society of Australia* 5: 1–15
- Jenkins, B.W. (1983). Redescriptions and relationship of *Siphonaria zelandica* Quoy and Gaimard with a description of *S. propria* sp. nov. (Mollusca: Pulmonata: Siphonariidae). *Journal of the Malacological Society of Australia* 6: 1–35
- Jenkins, B.W. (1984). A new siphonariid (Mollusca: Pulmonata) from south-western Australia. *Journal of the Malacological Society of Australia* 6: 113–123
- Johnston, R.M. (1880). Notes on the yellow limestone (travertine) of Geilston Bay with other fluviatile and lacustrine deposits in Tasmania and Australia, together with descriptions of two new fossil helices. *Papers and Proceedings of the Royal Society of Tasmania* 1879: 81–90
- Jones, H.D. (1973). The mechanism of locomotion of *Agriolimax reticulatus* (Mollusca: Gastropoda). *Journal of Zoology, London* 171: 489–498
- Jones, H.D. (1975). Locomotion. Pp. 1–32 in Fretter, V. & Peake, J.F. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. London: Academic Press
- Kendrick, G.W. (1978). New species of fossil nonmarine molluscs from Western Australia and evidence of Late Quaternary climatic change in the Shark Bay District. *Journal of the Royal Society of Western Australia* 60: 49–60
- Kendrick, G.W. & Sedgwick, E.H. (1973). A new introduced land snail for Western Australia. *Western Australian Naturalist* 12: 146–147
- Kendrick, G.W., Sedgwick, E.H. & Smith, B.J. (1971). The rediscovery of *Helix georgiana* Quoy & Gaimard, 1832 (Mollusca: Gastropoda) at Pemberton and the discovery of a related species in the Stirling Ranges, Western Australia. *Western Australian Naturalist* 12: 5–11
- Kendrick, G.W. & Wilson, B.R. (1975). Nomenclatural notes on the land snail genus *Bothriembryon* Pilsbry, 1894 (Pulmonata: Bulmulidae), with redescrptions of the type and two other species. *Records of the Western Australian Museum* 3: 295–325
- Kenny, R. & Smith, A. (1987). Distribution of *Onchidium damelii* Semper (Gastropoda, Onchidiidae). *Pacific Science* 41: 21–30
- Kenny, R. & Smith, A. (1988). Emergence behaviour of *Onchidium damelii* Semper, 1882 (Gastropoda, Onchidiidae). *Journal of the Malacological Society of Australia* 9: 19–20
- Borradaile, L.A., Potts, F.A., Eastham, L.E.S. & Saunders, J.T. (1958). *The Invertebrata: a manual for the use of students*. Cambridge University Press: Cambridge 3rd edn xvii 795 pp.
- Kerkut, G.A. & Walker, R.J. (1975). Nervous system, eye and statocyst. Pp. 165–244 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. Academic Press: London
- Kerney, M.P. & Cameron, R.A.D. (1979). *A Field Guide to the Land Snails of Britain and North-West Europe*. London: Collins 288 pp.
- Kershaw, R.C. (1979). Redescription of *Helicarion cuvieri* from southern Tasmania and *Helicarion freycineti* from New South Wales (Pulmonata: Helicarionidae). *Journal of the Malacological Society of Australia* 4: 145–156
- Kershaw, R.C. (1981a). The validity of the taxon *Bothriembryon tasmanicus* (Pulmonata: Bulimulidae). *Records of the Queen Victoria Museum* 73: 1–8
- Kershaw, R.C. (1981b). Redescription of genus *Helicarion* and of *Helicarion niger* (Quoy and Gaimard, 1832) from Victoria (Pulmonata: Helicarionidae). *Journal of the Malacological Society of Australia* 5: 17–31

17. PULMONATA

- Kershaw, R.C. (1983). The identity of *Helicarion freycineti* Férussac (Mollusca: Pulmonata). *Journal of the Malacological Society of Australia* 6: 59–61
- Kershaw, R.C. (1986). Anatomical notes of the land snail *Bothriembryon* (Pulmonata: Bulimulidae) from South Australia and Western Australia. *Records of the South Australian Museum* 19: 327–337
- Kershaw, R.C. (1987a). Type localities for six species of Tasmanian land molluscs (Pulmonata: Stylommatophora). *Papers and Proceedings of the Royal Society of Tasmania* 121: 57–68
- Kershaw, R.C. (1987b). Redescriptions of *Cystopelta petterdi* Tate, 1881 and *Cystopelta bicolor* Petterd and Hedley, 1909 (Pulmonata: Cystopeltidae). *Journal of the Malacological Society of Australia* 8: 51–70
- Kershaw, R.C. (1988a). A study of the Caryodidae (Pulmonata) Part I. *Anoglypta launcestonensis* (Reeve, 1853). *Records of the Queen Victoria Museum, Launceston* 93: 1–24
- Kershaw, R.C. (1988b). A study of the Caryodidae (Pulmonata) Part II. *Caryodes dufresni* (Leach, 1815). *Records of the Queen Victoria Museum, Launceston* 94: 1–27
- Kershaw, R.C. (1989). A study of the Caryodidae (Pulmonata) Part III: Subspecies of *Caryodes dufresni* (Leach, 1815). *Records of the Queen Victoria Museum, Launceston* 97: 1–25
- Kershaw, R.C. & Dartnall, A.J. (1972). The mollusc *Caryodes dufresni* in Tasmania. *Caryodes dufresni* (Leach) (Mollusca: Pulmonata). *Victorian Naturalist* 89: 111–118
- Kershaw, R.C. & Dartnall, A.J. (1975). The mollusc *Caryodes dufresni* in Tasmania. Part 2. *Victorian Naturalist* 92: 187–189
- Kershaw, R.C. & Smith, B.J. (1986). Description of two punctid snail genera from Tasmania (Mollusca: Pulmonata). *Victorian Naturalist* 103: 16–18
- Kisker, L.G. (1923). Über Anordnung und Bau der interstitiellen Binde-substanzen von *Helix pomatia* L. *Zeitschrift für Wissenschaftliche Zoologie* 121: 64–125
- Komai, T. & Emura, S. (1955). A study of population genetics on the polymorphic land snail *Bradybaena similis*. *Evolution* 9: 400–418
- Kondo, Y. (1943). Anatomical studies of three species of *Ouagapia* (Pulmonata, Agnatha, Paryphantidae). *Occasional Papers of the Bernice Pauahi Bishop Museum* 17: 229–248
- Ladd, H.S. (1958). Fossil land shells from Western Pacific atolls. *Journal of Paleontology* 32: 183–198
- Laidlaw, F.F. (1940). Notes on some specimens of the genus *Atopos* (Mollusca, Pulmonata) with microphotographs illustrating points in the anatomy of the genus. *Bulletin of the Raffles Museum* 16: 121–132
- Legrand, W. (1871). *Collections for a Monograph of Tasmanian Land Shells*. [s.n.] : Hobart Town 42 leaves
- Loch, I. (1981). A slug with an angle. *Australian Shell News* 33: 6
- Long, D.C. (1970). *Arion intermedius* (Normand) an introduced slug in Victoria. *Victorian Naturalist* 87: 170–172
- Long, D.C. (1972). Zonitid snails (Gastropoda: Pulmonata) introduced into Victoria. *Memoirs of the National Museum of Victoria* 33: 115–120
- Ludbrook, N.H. (1978). Quaternary molluscs of the western part of the Eucla Basin. *Bulletin of the Geological Survey of Western Australia* 125: 1–286
- Ludbrook, N.H. (1980). Non-marine molluscs from dolomitic limestones in the north of South Australia. *Transactions of the Royal Society of South Australia* 104: 83–92
- Ludbrook, N.H. (1984). Quaternary molluscs of South Australia. *Department of Mines and Energy, South Australia, Handbook* No. 9: 1–327
- Machin, J. (1975). Water relationships. Pp. 105–163 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. Academic Press : London
- MacPherson, J.H. & Gabriel, C.J. (1962). *Marine Molluscs of Victoria*. Melbourne University Press and National Museum of Victoria : Melbourne xv 475 pp.
- Malcolm, H.E. (1987). Invertebrate fauna of the Franklin River area, Tasmania. *Tasmanian Naturalist* 91: 1–7
- Malek, E.A. & Cheng, T.C. (1974). *Medical and Economic Malacology*. Academic Press : New York & London 398 pp.
- Mapstone, G.P. (1978). Egg capsules and early development in *Siphonaria diemenensis* (Quoy and Gaimard, 1833) and *Siphonaria baconi* (Reeve, 1856). *Journal of the Malacological Society of Australia* 4: 85–92
- Marcus, Ev. & Marcus, Er. (1965a). On Brazilian supratidal and estuarine snails. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Zoologia* 25: 19–82
- Marcus, Ev. & Marcus, Er. (1965b). On two Ellobiidae from southern Brazil. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo. Zoologia* 25: 425–453
- McAlpine, D. (1952). Notes on some Siphonariidae. *Proceedings of the Royal Zoological Society of New South Wales* 1951–52: 40–42
- McLauchlan, C.F. (1951). Basic work on the life cycle of some Australian snails. *Proceedings of the Royal Zoological Society of New South Wales* 1949–50: 26–36
- McLauchlan, C.F. (1954). Land shells originally introduced. *Australian Zoologist* 12: 40
- McMichael, D.F. (1959). A new genus and species of land snail from North Queensland. *Journal of the Malacological Society of Australia* 1(3): 31–32
- McMichael, D.F. (1967). Australian freshwater Mollusca and their probable evolutionary relationships: a summary of present knowledge. Pp. 123–149 in Weatherley, A.H. (ed.) *Australian Inland Waters and their Fauna: Eleven Studies*. Australian National University Press : Canberra
- McMichael, D.F. (1968). Non-marine Mollusca from Tertiary rocks in northern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 80: 133–157
- McMichael, D.F. & Iredale, T. (1959). The land and freshwater Mollusca of Australia. Pp. 224–245 in Keast, A., Crocker, R.L. & Christian, C.S. (eds) *Biogeography and Ecology in Australia. Monographiae Biologiae* 8. Junk : Den Haag
- Mead, A.R. (1950). Comparative genital anatomy of some African Achatinidae. *Bulletin of the Museum of Comparative Zoology* 105: 219–291
- Mead, A.R. (1961). *The Giant African Snail. A Problem in Economic Malacology*. University of Chicago Press : Chicago xvii 257 pp.
- Meer Mohr, J.C. van der (1949). On the reproductive capacity of the African or giant snail, *Achatina fulica* (Fér). *Treubia* 20: 1–10
- Meier-Brook, C. & Smith, B.J. (1975). *Glacidorbis* Iredale 1943, a genus of freshwater prosobranchs with a Tasmanian – southeast Australian – south Andean distribution. *Archiv für Molluskenkunde* 106: 191–198
- Mordan, P.B. (1984). Taxonomy and biogeography of southern Arabian Enidae (*sensu lato*) (Pulmonata: Pupillacea). Pp. 124–133 in Solem, A. & Bruggen, A.C. van (eds) *World-Wide Snails. Biogeographical Studies on Non-marine Mollusca*. E.J. Brill : Leiden
- Mordan, P.B. (1986). A taxonomic revision of the southern Arabian Enidae *sensu lato* (Mollusca: Pulmonata). *Bulletin of the British Museum (Natural History), Zoology* 50: 207–271
- Morton, J.E. (1955a). The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proceedings of the Zoological Society of London* 125: 127–168
- Morton, J.E. (1955b). The functional morphology of the British Ellobiidae (Gastropoda Pulmonata) with special reference to the digestive and reproductive systems. *Philosophical Transactions of the Royal Society of London, Series B* 239: 89–160
- Morton, J.E. (1979). *Molluscs*. Hutchinson & Co. : London 5th edn 264 pp.
- Musson, C.T. (1890). On the naturalised forms of land and freshwater Mollusca in Australia. *Proceedings of the Linnean Society of New South Wales* (2) 5: 883–896
- Naggs, F. (1989). *Gulella bicolor* (Hutton) and its implications for the taxonomy of streptaxids. *Journal of Conchology* 33: 165–168
- Nordsieck, H. (1992). Phylogeny and system of the Pulmonata. *Archiv für Molluskenkunde* 121: 31–52

- Odhner, N. (1917). Results of Dr E Mjöberg's Swedish Scientific Expeditions to Australia 1910–1913. XVII. Mollusca. *Kungliga Svenska Vetenskapsakademiens Handlingar* 52: 1–115
- Odhner, N.J. (1922). Mollusca from Juan Fernandez and Easter Island. Pp. 219–265 in Skottsberg, C. (ed.) *The Natural History of Juan Fernandez and Easter Island*. Vol. 3. Uppsala
- Parodiz, J.J. (1969). The Tertiary non-marine Mollusca of South America. *Annals of the Carnegie Museum* 40: 1–242
- Patterson, C.M. (1971). Taxonomic studies of the land snail family Succineidae. *Malacological Review* 4: 131–202
- Pawson, P.A. & Chase, R. (1984). The life cycle and reproductive activity of *Achatina fulica* (Bowdich) in laboratory culture. *Journal of Molluscan Studies* 50: 85–91
- Petterd, W.F. (1879a). *Monograph of the Land Shells of Tasmania*. Launceston Examiner: Launceston 55 pp.
- Petterd, W.F. (1879b). Colonising land shells. *Journal of Conchology* 2: 97–98
- Pilkington, M.C. & Pilkington, J.B. (1982). The planktonic veliger of *Amphibola crenata* (Gmelin). *Journal of Molluscan Studies* 48: 24–29
- Pilkington, M.C. & Pilkington, J.B. (1984a). Settlement in the New Zealand mud snail, *Amphibola crenata*. *Journal of the Royal Society of New Zealand* 14: 145–149
- Pilkington, M.C. & Pilkington, J.B. (1984b). The stimulus for metamorphosis of a high-shore pulmonate, *Amphibola crenata*. *Journal of the Royal Society of New Zealand* 14: 139–143
- Pilsbry, H.A. (1894). Pulmonata. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 9: 49–160
- Pilsbry, H.A. (1895–1896). Pulmonata, Bulimi. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 9 (36): 161–366; Vol. 10 (37–40): 1–213
- Pilsbry, H.A. (1897–1898). Pulmonata, Bulimuli. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 11 (41–44): 1–339
- Pilsbry, H.A. (1899). Pulmonata, Bulimulidae. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 12 (45–48): 1–258
- Pilsbry, H.A. (1900a). On the zoological position of *Partula* and *Achatinella*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1900: 561–567
- Pilsbry, H.A. (1900b). Pulmonata, Bulimulidae and Helicidae. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 13 (49–52): 1–253
- Pilsbry, H.A. (1901). Pulmonata, Bulimi, Bulimulidae. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 14 (53–55): 1–192
- Pilsbry, H.A. (1902). Pulmonata, Classification of Bulimulidae and index to volumes 10, 11, 12, 13 and 14. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 15 (57, 58): 1–128
- Pilsbry, H.A. (1904). Pulmonata, Achatinidae. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 16 (64, 64a): 193–329; Vol. 17 (65, 66): 1–112
- Pilsbry, H.A. (1905–1906). Pulmonata [Achatinidae, Stenogyrinae and Coliastinae]. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology: structural and systematic. With illustrations of the species*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 18 (69–71): 1–272
- Pilsbry, H.A. (1916–1918). Pulmonata. [Tortanellidae, Pupillidae]. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 22 (91, 92): 257–302; Vol. 23 (93): 129–302, (94–96): 1–380; Vol. 24 (97): 1–64
- Pilsbry, H.A. (1919–1920). Pulmonata. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Section, Academy of Natural Sciences: Philadelphia Series 2. Vol. 24 (98, 99): 65–224; Vol. 25 (100): 225–401; Vol. 26 (101): 1–64
- Pilsbry, H.A. (1919). A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo Expedition, 1909–1915. *Bulletin of the American Museum of Natural History* 40: 1–370
- Pilsbry, H.A. (1920–1921). Pulmonata. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Department, Academy of Natural Sciences: Philadelphia Series 2. Vol. 26 (101–104): 1–254
- Pilsbry, H.A. (1922–1926). Pulmonata. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Department, Academy of Natural Sciences: Philadelphia Series 2. Vol. (105, 106, 108): 1–369
- Pilsbry, H.A. (1927–1935). Pulmonata. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Department, Academy of Natural Sciences: Philadelphia Series 2. Vol. 28 (109–110): 1–160
- Pilsbry, H.A. (1939). Land Mollusca of North America (north of Mexico). *Monographs of the Academy of Natural Sciences of Philadelphia*, No. 3 1(1): 1–573
- Pilsbry, H.A. (1946). Land Mollusca of North America (north of Mexico). *Monographs of The Academy of Natural Sciences of Philadelphia* No. 3 2(1): 1–520
- Pilsbry, H.A. (1948). Land Mollusca of North America (North of Mexico). *Academy of Natural Sciences of Philadelphia, Monographs* No. 3 2(2): 521–1113
- Pilsbry, H.A. & Cooke, C.M. (1912–1914). Pulmonata, Achatinellidae. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Department, Academy of Natural Sciences: Philadelphia Series 2. Vol. 21 (84): 1–387; Vol. 15 (85–87): 1–176
- Pilsbry, H.A. & Cooke, C.M. (1915). Pulmonata, Achatinellidae. In Tryon, G.W. & Pilsbry, H.A. *Manual of Conchology*. Conchological Department, Academy of Natural Sciences: Philadelphia Series 2. Vol. 21 Supplement (89, 90): 1–128; Vol. 22 (88): 117–369, 400–428, with appendix by Alpheus Hyatt (pp. 370–399)
- Plesch, B., Janse, C. & Boer, H.H. (1975). Gross morphology and histology of the musculature of the freshwater pulmonate *Lymnaea stagnalis* (L.). *Netherlands Journal of Zoology* 25: 332–352
- Pokryszko, B.M. (1987). On aphylls in the Vertiginidae (Gastropoda: Pulmonata: Orthurethra). *Journal of Conchology* 32: 365–375
- Pokryszko, B.M. (1990). The Vertiginidae of Poland (Gastropoda: Pulmonata: Pupilloidea) – a systematic monograph. *Annales Zoologici* 43: 134–257
- Pokryszko, B.M. (1996). The Gastrocoptinae of Australia (Gastropoda: Pulmonata: Pupilloidea): systematics, distribution and origin. *Invertebrate Taxonomy* 10: 1085–1150
- Pomeroy, D.E. & Laws, H.M. (1967). The distribution of introduced snails in South Australia. *Records of the South Australian Museum* 15: 483–494
- Ponder, W.F. (1975). The occurrence of *Lymnaea* (*Pseudosuccinea*) *columella*, an intermediate host of *Fasciola hepatica*, in Australia. *Australian Veterinary Journal* 51: 494–495
- Ponder, W.F. (1986). Glacidorbidae (Glacidorbacea: Basommatophora), a new family and superfamily of operculate freshwater gastropods. *Zoological Journal of the Linnean Society* 87: 53–83
- Pötzsch, O. (1904). Über die entwicklung von niere, pericard und herz bei *Planorbis corneus*. *Zoologische Jahrbücher, Abteilung Anatomie* 20: 409–438
- Powell, A.W.B. (1949). The Paryphantidae of New Zealand. No. VI. Distribution, hybrids and new species of *Paryphanta*, *Rhytida* and *Schizoglossa*. *Records of the Auckland Institute and Museum* 3(6): 347–372
- Powell, A.W.B. (1950). Life history of *Austrosuccinea archeyi*, an annual snail, and its value as a post-glacial climatic indicator. *Records of the Auckland Institute and Museum* 4: 61–72

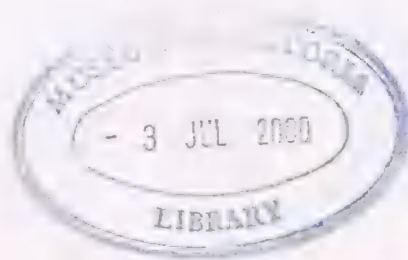
17. PULMONATA

- Quick, H.E. (1933). The anatomy of British Succineae. *Proceedings of the Malacological Society of London* 20: 295–318
- Quick, H.E. (1936). The anatomy of some African Succineae, and of *Succinea hungarica* Hazey, and *S. australis* Férussac for comparison. *Annals of the Natal Museum* 8: 19–45 f050703
- Quick, H.E. (1960). British slugs (Pulmonata: Testacellidae, Arionidae, Limacidae). *Bulletin of the British Museum (Natural History)*, Zoology 6: 103–226
- Quinn, G.P. (1983). Spawning and egg masses of *Siphonaria tasmanica* Tenison Woods, 1876 from Victoria. *Journal of the Malacological Society of Australia* 6: 81–82
- Quoy, J.R.C. & Gaimard, J.P. (1824). in Freycinet, M.L. de (ed.) *Voyage Autour du Monde, entrepris par ordre du Roi, sous le Ministère et conformément aux la instructions de S. Exc. M. le Viscomte du Bouchage, Secrétaire d'Etat au Département de la Marine, exécute sur les Corvettes de S.M. l'Uraïne et la Physicienne, pendant les années 1817–1820*. Zoologie. Pillet Aîné : Paris 671 pp.
- Raven, C.P. (1975). Development. Pp. 367–400 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. Academic Press : London
- Richardot, M. (1977a). Ecological factors inducing estivation in the freshwater limpet *Ferrissia wautieri* (Basommatophora : Ancyliidae) I. Oxygen content, organic matter content and pH of the water. *Malacological Review* 10: 7–13
- Richardot, M. (1977b). Ecological factors influencing estivation in the freshwater limpet *Ferrissia wautieri* (Basommatophora : Ancyliidae). II. Photoperiod, light intensity and water temperature. *Malacological Review* 10: 15–30
- Richardson, J.E. (1970). Dr James Cox: Conchologist 1834–1912. *Proceedings of the Royal Zoological Society of New South Wales* 1969–70: 71–83
- Riedl, R. (1960). Beiträge zur Kenntnis der *Rhodope veranii*. 2. Entwicklung. *Zeitschrift für Wissenschaftliche Zoologie* 163: 237–316
- Rigby, J.E. (1963). Alimentary and reproductive systems of *Oxychilus cellarius* (Müller) (Stylommatophora). *Proceedings of the Zoological Society of London* 141: 311–359
- Rigby, J.E. (1965). *Succinea putris*: a terrestrial opisthobranch mollusc. *Proceedings of the Zoological Society of London* 144: 445–486
- Runham, N.W. (1963). The histochemistry of the radulas of *Acanthochiton communis*, *Lymnaea stagnalis*, *Helix pomatia*, *Scaphander lignarius* and *Archidoris pseudoargus*. *Annales d'Histochimie* 8: 433–442
- Runham, N.W. (1975). Alimentary canal. Pp. 53–104 in Fretter, V. & Peake, J.F. (eds) *Pulmonates. Vol. 1. Functional anatomy and physiology*. London : Academic Press
- Runham, N.W. & Hunter, P.J. (1970). *Terrestrial Slugs*. Hutchinson University Library : London 184 pp.
- Runham, N.W., Isarankura, K. & Smith, B.J. (1965). Methods for narcotizing and anaesthetizing gastropods. *Malacologia* 2: 231–238
- Salvini-Plawen, L. von (1970). Zur systematischen Stellung von Soleolifera und Rhodope (Gastropoda, Euthyneura). *Zoologische Jahrbücher, Abteilung Systematik* 97: 285–299
- Schumann, W. (1911). Über die Anatomie und die systematische Stellung von *Gadinia peruviana* Sowerby und *Gadinia garnoti* Payraudeau. *Zoologische Jahrbücher, Supplement* 13. Fauna Chilensis 4: 1–88
- Scott, B. (1990). Fabians of the forest. *Australian Natural History* 23: 220–224
- Selenka, E. (1865). Zwei neue nachtschnecken aus Australien (*Limax pectinatus* und *bicolor*). *Malakozoologische Blätter* 12: 105–110
- Semper, K.G. (1885). Onchididae In *Reisen im Archipel der Philippinen* 3: 251–327
- Shea, M. (1982). First pleurodiscid snail in Australia. *Australian Shell News* 40: 6
- Shea, M. (1983). A checklist of landsnails from the Sydney area. *Australian Shell News* 44: 6–7
- Short, J.W. & Potter, D.G. (1987). *Shells of Queensland and the Great Barrier Reef. Marine Gastropods*. Robert Brown & Associates : Bathurst, New South Wales iv 135 pp.
- Simpson, R.D. & Harrington, S.A. (1985). Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevittorina caliginosa* and *Macquariella hamiltoni* (Littorinidae) from Macquarie Island (sub-Antarctic). *Journal of the Malacological Society of Australia* 7: 17–28
- Simroth, H.R. (1889). Über einige *Vaginula*-Arten. *Zoologischer Anzeiger* 12: 551–556, 574–578.
- Smith, A. & Kenny, R. (1987). Reproduction and development of *Onchidium damelii* Semper, 1882. *Journal of the Malacological Society of Australia* 8: 37–39
- Smith, B.J. (1965). The secretions of the reproductive tract of the garden slug *Arion ater*. *Annals of the New York Academy of Sciences* 118: 997–1014
- Smith, B.J. (1966a). Maturation of the reproductive tract of *Arion ater* (Pulmonata: Arionidae). *Malacologia* 4: 325–349
- Smith, B.J. (1966b). The structure of the central nervous system of the slug *Arion ater* L., with notes on the cytoplasmic inclusions of the neurones. *Journal of Comparative Neurology* 126: 437–451
- Smith, B.J. (1967a). Correlation between neurosecretory changes and maturation of the reproductive tract of *Arion ater* (Stylommatophora: Arionidae). *Malacologia* 5: 285–298
- Smith, B.J. (1967b). Notes on the distribution of the dune-snail *Theba pisana* Muller at Portsea Back Beach. *Victorian Naturalist* 84(9): 267–270
- Smith, B.J. (1970). Notes on the anatomy of *Victaphanta atramentaria* (Shuttleworth) and *V. compacta* (Cox and Hedley), and the designation of a neotype for *V. atramentaria*. *Journal of the Malacological Society of Australia* 2: 13–21
- Smith, B.J. (1971). Carnivorous snails of the family Paryphantidae. *Australian Natural History* 17: 55–58
- Smith, B.J. (1973). A new species of snail from Lake Pedder, Tasmania, belonging to the family Valvatidae. *Journal of the Malacological Society of Australia* 2: 429–434
- Smith, B.J. (1979a). A new species of *Glacidorbis* (?Hydrobiidae: Gastropoda) from Great Lake, Tasmania. *Journal of the Malacological Society of Australia* 4: 121–127
- Smith, B.J. (1979b). Notes on two new species of rhytidid snails from Lizard Island, North Queensland. *Records of the Australian Museum* 32: 421–433
- Smith, B.J. (1980). Molluscs on Lake Mountain. *Victorian Naturalist* 97: 76
- Smith, B.J. (1981). Introduced non-marine Mollusca in Australia. *Victorian Naturalist* 98: 24–27
- Smith, B.J. (1984). Regional endemism of the south-eastern Australian land mollusc fauna. Pp. 172–188 in Solem, A. & Van Bruggen, A.C. (eds) *World-wide Snails: Biogeographical Studies on Non-marine Mollusca*. E.J. Brill and W. Backhuys : Leiden
- Smith, B.J. (1985). A range extension of the snail *Glacidorbis hedleyi* Iredale, 1943 in Victoria. *Victorian Naturalist* 103: 123–126
- Smith, B.J. (1987). Description of a new genus of carnivorous snail (Mollusca: Rhytididae). *Victorian Naturalist* 104: 86–90
- Smith, B.J. (1989). Travelling snails. *Journal of Medical and Applied Malacology* 1: 195–204
- Smith, B.J. (1992). Non-marine Mollusca. in Houston, W.W.K. (ed.) *Zoological Catalogue of Australia. Vol. 8*. Australian Government Publishing Service : Canberra xii 405 pp.
- Smith, B.J., Black, J.H. & Shepherd, S.A. (1989). Molluscan egg masses and capsules. Pp. 841–890 in Shepherd, S.A. & Thomas, I.M. *Marine Invertebrates of Southern Australia. Part II*. South Australian Government Printing Division : Adelaide
- Smith, B.J. & Dartnall, A.J. (1976). Veronicellid slugs in the Northern Territory with notes on other land molluscs. *Journal of the Malacological Society of Australia* 3: 186
- Smith, B.J. & Djajasasmita, M. (1988). The land molluscs of the Krakatau Islands, Indonesia. *Philosophical Transactions of the Royal Society of London B* 323: 379–400

- Smith, B.J. & Kershaw, R.C. (1972). Tasmanian snail referred to the genus *Victaphanta* (Stylommatophora: Paryphantidae). *Memoirs of the National Museum of Victoria* 33: 111–114
- Smith, B.J. & Kershaw, R.C. (1979). *Field Guide to the Non-Marine Molluscs of South Eastern Australia*. Australian National University Press : Canberra x 285 pp.
- Smith, B.J. & Kershaw, R.C. (1981). *Tasmanian Land and Freshwater Molluscs*. Fauna of Tasmania Handbook Series, No. 5. University of Tasmania : Hobart 148 pp.
- Smith, B.J. & Kershaw, R.C. (1985). Description of three Tasmanian charopid genera (Pulmonata: Mollusca) with notes on their types. *Records of the Queen Victoria Museum* No. 88: 1–14
- Smith, B.J. & Plant, R.J. (1981). Differentiating the left-handed freshwater snails of south-eastern Australia. *Victorian Naturalist* 98: 257–260
- Solem, A. (1959a). Systematics of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana Zoology* 43: 1–238
- Solem, A. (1959b). Zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana Zoology* 43: 241–323
- Solem, A. (1964a). New records of New Caledonian non-marine mollusks and an analysis of the introduced mollusks. *Pacific Science* 18: 130–137
- Solem, A. (1964b). *Amimopina*, an Australian enid land snail. *The Veliger* 6: 115–120
- Solem, A. (1966). Some non-marine mollusks from Thailand, with notes on classification of the Helicarionidae. *Spolia Zoologica Musei Hauniensis* 24: 1–110
- Solem, A. (1969). Basic distribution of non-marine molluscs. Pp. 231–247 in Rao, K.V. (convenor) *Proceedings of the Symposium on Mollusca, Marine Biological Association of India*. Symposium series 3(1). Mandapan Camp : Marine Biological Association of India
- Solem, A. (1972a). *Tekoulina*, a new viviparous tornatellinid land snail from Rarotonga, Cook Islands. *Proceedings of the Malacological Society of London* 40: 93–114
- Solem, A. (1972b). Malacological applications of scanning electron microscopy. II. Radula structure and function. *The Veliger* 14: 327–336
- Solem, A. (1973). Convergence in pulmonate radulae. *The Veliger* 15: 165–171
- Solem, A. (1974). *The Shell Makers: Introducing Mollusks*. John Wiley & Sons : New York xii 289 pp.
- Solem, A. (1975). *Polygyriscus virginianus* (Burch, 1947), a helicodiscid land snail (Pulmonata: Helicodiscidae). *The Nautilus* 89: 80–86
- Solem, A. (1976). Endodontoid land snails from Pacific Islands. Part I. Family Endodontidae. *Fieldiana: Zoology, Special Publication* pp. 1–508, 208 figs
- Solem, A. (1978a). Classification of the land Mollusca. Pp. 49–97 in Fretter, V. & Peake, J. (eds) *Pulmonates. Vol. 2A. Systematics, evolution and ecology*. Academic Press : London
- Solem, A. (1978b). Cretaceous and early Tertiary camaenid land snails from western North America (Mollusca: Pulmonata). *Journal of Paleontology* 52: 581–589
- Solem, A. (1979a). A theory of land snail biogeography patterns through time. Pp. 225–249 in van der Spoel, S., Bruggen, A.C. van & Lever, J. (eds) *Pathways in Malacology*. Sixth European Malacology Congress Amsterdam, 1977. Junk : The Hague
- Solem, A. (1979b). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). I. Taxa with trans-Australian distribution. *Records of the Western Australian Museum, Supplement* No. 10: 5–142
- Solem, A. (1981a). Small land snails from northern Australia. I. Species of *Gyliotrachela* Tomlin, 1930 (Mollusca: Pulmonata, Vertiginidae). *Journal of the Malacological Society of Australia* 5: 87–100
- Solem, A. (1981b). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale, 1933. *Records of the Western Australian Museum, Supplement* No. 11: 147–320
- Solem, A. (1981c). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from the Ningbing Ranges and nearby areas. *Records of the Western Australian Museum, Supplement* No. 11: 321–425
- Solem, A. (1982). Small land snails from northern Australia. II. Species of *Westracystis* Iredale, 1939 (Mollusca: Pulmonata, Helicarionidae). *Journal of the Malacological Society of Australia* 5: 175–193
- Solem, A. (1983a). *Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra) Part II. Families Punctidae and Charopidae, Zoogeography*. Field Museum Press : Chicago 336 pp.
- Solem, A. (1983b). First record of *Amphidromus* from Australia, with anatomical notes on several species (Mollusca: Pulmonata: Camaenidae). *Records of the Australian Museum* 35: 153–166
- Solem, A. (1984a). Small land snails from Northern Australia, III: Species of Helicodiscidae and Charopidae. *Journal of the Malacological Society of Australia* 6: 155–179
- Solem, A. (1984b). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale, 1933 and related genera. *Records of the Western Australian Museum, Supplement* No. 17: 427–705
- Solem, A. (1985a). Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley genera and addenda to the Kimberley. *Records of the Western Australian Museum, Supplement* No. 20: 707–981
- Solem, A. (1985b). Simultaneous character convergence and divergence in Western Australian land snails. *Biological Journal of the Linnean Society* 24: 142–163
- Solem, A. (1986a). Pupilloid land snails from the south and mid-west coasts of Australia. *Journal of the Malacological Society of Australia* 7: 95–124
- Solem, A. (1986b). Origin and diversification of pulmonate land snails. Pp. 269–293 in Trueman, E.R. & Clarke, M.R. (eds) *The Mollusca. Vol. 10*. Academic Press : London
- Solem, A. (1988a). Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, north-east Kimberley, Western Australia. *Journal of the Malacological Society of Australia* 9: 59–113
- Solem, A. (1988b). Non-camaenid land snails of the Kimberley and Northern Territory, Australia. I. Systematics, affinities and ranges. *Invertebrate Taxonomy* 2: 455–604
- Solem, A. (1988c). New camaenid land snails from the northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia* 9: 27–58
- Solem, A. (1989). Native and introduced Australian subulinid land snails: competition and coexistence. Unpublished paper presented at the Ninth International Malacological Congress, Edinburgh, 1986
- Solem, A. (1991). Land snails of Kimberley rainforest patches and biogeography of all Kimberley land snails. Pp. 145–246 in McKenzie, N.L., Johnston, R.B. & Kendrick, P.G. (eds) *Kimberley Rainforests of Australia*. Surrey Beatty & Sons : Chipping Norton, New South Wales
- Solem, A. (1992). Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Parts 1 & 2. *Records of the South Australian Museum Monograph Series* No. 2: 1–425
- Solem, A. (1993). Camaenid Land Snails from Western and Central Australia (Mollusca: Pulmonata: Camaenidae). VI. Taxa from the Red Centre. *Records of the Western Australian Museum, Supplement* No. 43: 983–1459
- Solem, A. & Christensen, C.C. (1984). Camaenid land snail reproductive cycle and growth patterns in semiarid areas of north-western Australia. *Australian Journal of Zoology* 32: 471–491
- Solem, A. & McKenzie, N.L. (1991). The composition of land snail assemblages in Kimberley rainforests. Pp. 247–263 in McKenzie, N.L., Johnston, R.B. & Kendrick, P.G. (eds) *Kimberley Rainforests of Australia*. Surrey Beatty & Sons : Chipping Norton, New South Wales

- Solem, A. & Yochelson, E.L. (1979). North American Palaeozoic land snails, with a summary of other Palaeozoic non-marine snails. *United States Geological Survey, Professional Paper* 1072, pp. i-iii, 1-42
- Sommerville, B.A. (1973). The circulatory physiology of *Helix pomatia*. 1. Observations on the mechanism by which *Helix* emerges from its shell and on the effects of body movements on cardiac function. *Journal of Experimental Biology* 59: 275-282
- Spratt, D.M. (1979). A taxonomic revision of the lungworms (Nematoda: Metastrongyloidea) from Australian marsupials. *Australian Journal of Zoology Supplementary Series* 67: 1-45
- Stanisic, J. (1981a). The carnivorous land snail *Gulella* (*Huttonella*) *bicolor* (Hutton, 1934) in Australia. (Pulmonata: Streptaxidae). *Journal of the Malacological Society of Australia* 5: 84-86
- Stanisic, J. (1981b). *Helix parramattensis* Cox, 1864: a synonym of *Euconulus* (*Euconulus*) *fulvus* (Müller, 1774). (Pulmonata: Euconulidae). *Journal of the Malacological Society of Australia* 5: 81-83
- Stanisic, J. (1982). The terrestrial Molluscs. Pp. 19-23 in Monteith, G.B. (ed.) *1981 Bellenden Ker Expedition, Interim Field Report*. Queensland Museum: Brisbane 30 pp.
- Stanisic, J. (1987). Studies on the Charopidae of tropical and subtropical Australia. I. *Oreokera*: a primitive genus from the high mountains of North Queensland (Mollusca: Pulmonata: Charopidae). *Journal of the Malacological Society of Australia* 8: 1-21
- Stanisic, J. (1988). A re-evaluation of the relationships of *Helix* (*Thalassia*) *gaydahensis* Brazier, 1875 (Mollusca, Pulmonata, Helicarionidae). *Memoirs of the Queensland Museum* 25: 475-479
- Stanisic, J. (1990). Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum* 30: 1-241
- Stanisic, J. (1993a). The identity of *Helicarion semoni* Marten, 1894: a large semi-slug from the Wet Tropics, northeastern Queensland (Pulmonata: Helicarionidae). *Memoirs of the Queensland Museum* 34: 1-9
- Stanisic, J. (1993b). *Danielleilona* gen. nov. from the Wet Tropics, northeastern Queensland (Pulmonata: Charopidae). *Memoirs of the Queensland Museum* 34: 11-20
- Stanisic, J. (1993c). *Lenwebbia paluma* sp. nov., from the Wet Tropics, northeastern Queensland (Pulmonata: Charopidae). *Memoirs of the Queensland Museum* 34: 21-26
- Stanisic, J. (1993d). *Eungarion mcdonaldi* gen. et sp. nov., a montane semi-slug from mideastern Queensland rainforests (Pulmonata: Helicarionidae). *Memoirs of the Queensland Museum* 34: 27-34
- Stanisic, J. (1994a). An ecologic and biogeographic study of a new Tertiary land snail from mideastern Queensland (Pulmonata: Caryodidae). *Memoirs of the Queensland Museum* 35: 241-247
- Stanisic, J. (1994b). The distribution patterns and species diversity of land snails in eastern Australia. *Memoirs of the Queensland Museum* 36: 207-214
- Stanisic, J. (1996a). New land snails from boggomoss environments in the Dawson Valley, southeastern Queensland (Eupulmonata: Charopidae and Camaenidae). *Memoirs of the Queensland Museum* 39: 343-354
- Stanisic, J. (1996b). A new camaenid land snail from the Wet Tropics Biogeographic Region, northeastern Queensland (Eupulmonata, Camaenidae). *Memoirs of the Queensland Museum* 39: 355-363
- Steenberg, C.M. (1918). Anatomie des *Acanthinula* et des *Vallonia*. Les organes génitaux. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 69: 1-15
- Strzelecki, P.E. de (1845). *Physical description of New South Wales and Van Dieman's Land accompanied by a geological map, section, and diagrams, and figures of the organic remains*. Longman, Brown, Green & Longmans: London 462 pp.
- Tate, R. (1881). On some Australian slugs, chiefly Tasmanian. *Papers and Proceedings of the Royal Society of Tasmania* 1880: 15-18
- Tenison Woods, J.E. (1877). On Tasmanian *Siphonaria*, including a new species. *Papers and Proceedings of the Royal Society of Tasmania* 1879: 99-100
- Thompson, T. (1973). Euthyneuran and other molluscan spermatozoa. *Malacologia* 14: 167-206, addendum 443-444
- Tillier, S. (1984a). Patterns of digestive tract morphology in the limacisation of helicarionid, succineid and athoracophorid snails and slugs (Mollusca: Pulmonata). *Malacologia* 25: 173-192
- Tillier, S. (1984b). Relationships of gymnomorph gastropods (Mollusca: Gastropoda). *Zoological Journal of the Linnean Society* 82: 345-362
- Tillier, S. (1989). Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylommatophora). *Malacologia* 30: 1-303
- Tillier, S. & Ponder, W.F. (1992). New species of *Smeagol* from Australia and New Zealand, with a discussion on the affinities of the genus (Gastropoda: Pulmonata). *Journal of Molluscan Studies* 58: 135-155
- Tomba, A. (1979). Oviparity, egg retention and ovoviviparity in pulmonates. *Journal of Molluscan Studies* 45: 155-160
- Tomba, A. (1984). Land snails (Stylommatophora). Pp. 47-140 in Tomba, A.S., Verdonk, N.H. & Van den Biggelaar, J.A.M. (eds) *The Mollusca. Vol. 7. Reproduction*. Academic Press: New York
- Trappman, W. (1916). Die musculatur von *Helix pomatia* L. *Zeitschrift für Wissenschaftliche Zoologie* 115: 489-585
- Tryon, G.W. (1885). Pulmonata. *Manual of Conchology*. Second series 1: 1-364
- Van Mol, J.-J. (1967). Etude morphologique et phylogénétique du ganglion cérébroïde des gastéropodes pulmonés (Mollusques). *Mémoires de l'Académie Royal de Belgique, Classe des Sciences* 37: 1-168
- Van Mol, J.-J. (1973). Notes anatomiques sur les Helicarionidae (Mollusques, Gastéropodes, Pulmonés). II. Etudes des genres *Pseudostenia*, *Dyakia*, *Helicarion* et comprennent la description de *Papuarion*, genre nouveau. Discussion sur la classification des Helicarionidae et les affinités des Urocyclidae. *Annales de la Société Royale Zoologique de Belgique* 103: 209-237
- Van Mol, J.-J. (1974). Evolution phylogénétique du ganglion cérébroïde chez les gastéropodes pulmonés. *Halictis* 4: 77-86
- Vaught, K.C. (1989). *A Classification of the Living Mollusca*. American Malacologists Incorporated: Florida 195 pp. Edited by Abbott, R.T. & Boss, K.J.
- Venmans, L.A.W.C. (1957). A species of *Ferussacia* in South Australia. *Journal of the Malacological Society of Australia* 1(1): 36-44
- Verdcourt, B. (1961). Notes on east African Enidae. *Journal of Conchology* 25: 9-14
- Verdonk, N.H. & Biggelaar, J.A.M. van den (1983). Early development and the formation of the germ layers. Pp. 91-122 in Verdonk, N.H. & Biggelaar, J.A.M. van den (eds) *The Mollusca. Vol. 3. Development*. Academic Press: New York
- Vincent, C., Griffond, B., Wijdenes, J. & Gomot, L. (1984). Contrôl d'une glande endocrine: les corps dorsaux par le système nerveux central chez *Helix aspersa*. *Compte Rendus Hebdomadaires des Séances, Académie des Sciences, Paris* (3) 299: 421-426
- Walker, G. (1969). Studies on digestion of the slug *Agriolimax reticulatus* (Müller), (Mollusca, Pulmonata, Limacidae). Unpublished PhD thesis, University of Wales: Bangor
- Walker, G. (1972). The digestive system of the slug *Agriolimax reticulatus* (Müller): experiments on phagocytosis and nutrient absorption. *Proceedings of the Malacological Society of London* 40: 33-43
- Walker, J.C. (1984). Geographical relationships of the buliniform planorbids of Australia. Pp. 189-197 in Solem, A. & Van Bruggen, A.C. (eds) *World-wide Snails: biogeographical studies on non-marine Mollusca*. E.J. Brill and W. Backhuys: Leiden
- Walker, J.C. (1988). Classification of Australian buliniform planorbids (Mollusca: Pulmonata). *Records of the Australian Museum* 40: 61-89

- Warburg, M.R. (1965). On the water economy of some Australian land snails. *Proceedings of the Malacological Society of London* 36: 297-305
- Watson, B.J. (1985). The giant African snail in Australia. Pest or nuisance? *Queensland Agricultural Journal* 3: 7-10
- Watson, H. (1920). The affinities of *Pyramidula*, *Patulastra*, *Acanthinula* and *Vallonia*. *Proceedings of the Malacological Society of London* 14: 6-30
- Wells, F.E. (1984). *A Guide to the Common Molluscs of South-western Australian Estuaries*. Western Australian Museum : Perth 112 pp.
- Wells, S.M., Pyle, R.M. & Collins, N.M. (1983). *The IUCN Invertebrate Red Data Book*. IUCN : Gland, Switzerland 632 pp.
- Whitney, M.E. (1940). The hermaphrodite gland and germ cells of *Vallonia pulchella*. Müll. *Papers of the Michigan Academy of Science* 26: 311-338
- Woolacott, L. (1945). The establishment of *Salinator fragilis* Lamarck and *Salinator solida* von Martens as two distinct species in Australia. *Proceedings of the Royal Zoological Society of New South Wales* 1944-45: 35-38
- Yonge, C.M. (1958). Observations in life of the pulmonate limpet *Trimusculus (Gadinia) reticulatus* (Sowerby). *Proceedings of the Malacological Society of London* 33: 31-37
- Zilch, A. (1959). Euthyneura. in Schindewolf, O.H. (ed.) *Handbuch der Paläozoologie*. Bornträger : Berlin-Zehlendorf Bd 6.II.2. xii 834 pp.



GLOSSARY

Definitions and descriptions of terms used in this volume have been limited to those which would generally require reference to specialist literature. Thus terms listed in standard dictionaries have been omitted, as have terms that are interpreted readily either from their component parts (for example, 'hinge teeth') or their context. Exceptions to these limits are terms that are in everyday use but have a specific meaning in the volume unrelated to their general use.

Many of the terms are defined directly from the present text. The several sources listed below were most valuable in resolving definitions.

abanal gills: in polyplacophorans, the condition in which gills are added only in a direction anterior to the first gill pair of the juvenile; in consequence, size decreases anteriorly – the posteriormost gill is largest; compare **adanal gills**.

abapertural: away from the aperture of a gastropod.

abapical: away from the apex (= 'anterior' in high-spined gastropods).

aboral: away from the mouth.

abaxial: on the opposite side of, or directed away from, the axis of an organism.

abyssal: oceanic waters between depths of 4000 m and 6000 m.

accessory boring organ: present on proboscis of Naticidae and the anterior sole of muricids; secretes acid or enzymes in conjunction with the radula to bore through the shell of prey.

accessory gill: gill developed in mantle cavity of some basommatophoran pulmonates; also termed a **secondary gill** or **pseudobranch**.

acetabuliferous arms: suckered, buccal appendages used for feeding in the Pneumodermatidae, Gymnosomata.

acleioproctic: anus opens to exterior in the inter-hepatic space alongside the heart; used previously in superfamilial division of Aeolidina; see also **cleioproctic** and **pleuroproctic**.

acrembolic proboscis: the proboscis, when not in use, is introverted by retractor muscles attached at midlength; compare **pleurembolic proboscis**.

acrosome: membrane-limited organelle at apex of spermatozoon head, covering the anterior surface of the nucleus; secretes enzymes thought to facilitate sperm entry.

actinodont: hinge dentition in bivalves in which teeth radiate from the beak; the outer ones are longer and lie close to the dorsal shell margin.

adanal gills: in polyplacophorans, the condition in which gills are added anterior to, and posterior to, the first gill pair of the juvenile; as a result gill size decreases anteriorly and posteriorly; compare **abanal gills**.

adapertural: towards the aperture of a gastropod.

adapical: towards the apex; = 'posterior' in high-spined gastropods.

adaxial: on the same side, or directed towards, the axis of an organism.

adductor muscle: joins and closes valves in bivalves, working in opposition to the ligament; **dimyarian** bivalves have anterior and posterior adductor muscles, which may be equal in size (**homomyarian** = **isomyarian**), or the anterior muscles are significantly smaller (**heteromyarian** = **anisomyarian**); bivalves with a single posterior adductor muscle are **monomyarian**.

adductor muscle scar: defined area where an adductor muscle of a bivalve attaches to the interior of the valve.

adoral: towards the mouth.

aesthete: microscopic sensory and/or secretory structure in tegmentum of polyplacophorans; comprises a **megalaesthete** from which arises a variable number of finer **micraesthetes**.

aestivation: state of dormancy undergone by some pulmonates during hot, dry conditions; analogous to **hibernation**.

afferent membrane: links the dorsal surface of the ctenidial axis with the mantle roof and carries the afferent branchial vessels bringing blood to the gill.

alate: winged.

Albian: uppermost stage in Lower Cretaceous in European stratigraphic system (Middle Cretaceous of some authors); above **Aptian**, below **Cenomanian** of Upper Cretaceous.

albumen gland: the proximal portion, relative to the gonad, of the glandular **pallial oviduct**; provides extra-embryonic nutritive layer around the egg; see also **capsule gland** and **mucous gland**.

alivincular ligament: flat ligament located between the umbones and the non-fibrous layer extending beyond the margins of the internal fibrous layer or **resilifer**.

allomones: metabolites used as defensive chemicals.

allosperm: = **exogenous sperm**.

allozymes: enzyme forms with the same activity, which differ slightly in amino acid sequence, produced at a single locus by different alleles.

alternative hermaphroditism: erratic sex-changes undertaken by an individual.

GLOSSARY

- ammonotelic:** nitrogenous waste excreted primarily as ammonium ions.
- amoebocytes:** mobile cells in tissues and body fluids; active in assimilation and excretion.
- amphidetic:** see *ligament*.
- ampulla:** enlarged part of *coelomic gonoduct*, distal to the *ovotestis*, in which *endogenous sperm* are stored in *opisthobranchs*; see also *seminal vesicle*.
- anachomata:** see *chomata*.
- anal sinus:** notch, slot or embayment on outer lip of *gastropods*, typically at or above periphery; allows excretion of waste products.
- anastrophic:** *protoconch* coiled about the same axis as the *teleoconch* and nucleus directed towards base of shell.
- androdiaulic:** *diaulic* reproductive system in which the *oviduct* and *vagina* are combined, and the *vas deferens* is separate; see *oodiaulic*.
- anisakiasis:** parasitic infection from raw seafood containing *nematodes*, especially *Anisakis* species.
- anisomyarian:** see *adductor muscles*.
- anisostrophic:** asymmetrically coiled.
- annulus:** thin, ring-shaped *endosiphuncular* deposit on inner surface of *septal neck* in *Nautiloidea*.
- antemucronal area:** the central area of the *tail valve* of a *polyplacophoran*, anterior to the *mucro*.
- anterior canal** see *siphonal canal*.
- anthropochory:** dispersal of plant and animal disseminules by humans.
- antiboreal:** see *austral*.
- anti-feedants:** anti-predatory chemicals used for defensive purposes.
- apertural sinus:** recurved notch in margin of *aperture*.
- aperture:** in *gastropods* and *nautiloids*, the single, large, terminal orifice through which the head-foot is extruded; in *scaphopods*, the anterior, larger orifice through which the *foot* and *captacula* are extruded, or the smaller posterior *aperture*.
- apex:** narrow, first-formed part of the *gastropod* shell, typically bearing a *protoconch*; in *scaphopods*, the posterior, narrower orifice, modified by slits or *notches* in some taxa; posterior, narrow end of *scaphopod*, *gastropod* or *nautiloid* shell; equivalent to *beak* in *bivalves*.
- aphally:** absence of a penis.
- apical tube:** see *pipe*.
- apocrine gland:** special gland on penis of some *caenogastropods*.
- apomorphy:** an advanced or derived feature; compare *plesiomorphy*.
- apophysis:** articulatory protuberance of the shell in 'prosobranchs'; projection for muscle attachment in *Heterodonta*, especially *pedal muscle* in *Pholadoidea*; *sutural lamina* of *polyplacophorans*.
- aposematic colouration:** protective or defensive colouration.
- Aptian:** stage in the mid Lower Cretaceous in the European stratigraphic system (Lower and Middle Cretaceous of some authors); above the *Neocomian* series *Barrenian*, and below the *Albian* stage.
- apyrene spermatozoa:** see *paraspermatozoa*.
- aquasperm:** spermatozoa with a short head (*acrosome* and *nucleus*), short *middle piece* and a *flagellum*, and released into surrounding water; *ect-aquasperm* fertilise eggs external to the body; fertilisation by *ent-aquasperm* occurs within the mantle cavity.
- aragonite:** orthorhombic calcium carbonate, differing in crystalline structure from, and dimorphic with, *calcite*.
- arcuate:** curved or arched like a bow.
- Arenigian:** European stage in Lower Ordovician; above *Tremadocian*, below *Llanvinian*.
- arms:** the eight head appendages of *cephalopods*.
- armature:** defensive or offensive structures of an organism, as in suckers and hooks on arms of *cephalopods*.
- articulamentum** : the inner, dense shell layer of *polyplacophoran valves*, extending beyond the *tegumentum* to form the *sutural laminae* and *insertion plates*, which are embedded and attached to *girdle*; sometimes subdivided into two layers, an outer *articulamentum* (sensu stricto), and an inner *hypostracum*.
- ascus:** ventral sac-like structure in exterior buccal cavity of *sacoglossans*, into which the active and used parts of the *radula* ribbon descend; may retain discarded *radular* teeth.
- asiphonate:** lacking siphons.
- aspidobranch:** = *bipectinate*: refers to *ctenidia* bearing two rows of gill leaflets.
- atrium:** receiving (first) chamber, such as the *gastropod* heart, the *opisthobranch* vaginal entrance, the common entrance to the male and female components of the *pulmonate* reproductive system, and the *oesophagus* in some *pulmonates*.
- aulacopodous:** *pedal groove* situated well above the lateral angle of the foot of *pulmonates*; see also *holopodous*.
- auricle:** = *atrium* of the heart; ear-like lateral extension of *bivalve* shell on each side of *umbo*.
- auriculate:** ear-like appendages.
- auriform:** ear-shaped.
- austral:** pertaining to southern hemisphere cold temperate regions.
- Australian Region:** one of six global zoogeographical regions; comprises New Guinea, Australia, New Zealand and the westernmost groups of South Pacific islands, and, depending on the taxon, parts of the Indonesian Archipelago east of Java and Sulawesi.
- autapomorphy:** a derived feature or character state unique to a particular taxon.
- autosperm:** = *endogenous sperm*.
- autospermal groove:** = *seminal groove*.
- autotomy:** deliberate loss of body parts: *hectocotylus* used by some *cephalopods* during sperm transfer; when disturbed, presumably to distract predators, including the *metapodium*, *parapodia* and *cerata* in some *gastropods*, *pallial tentacles* and *siphons* of some *bivalves*, arms of some *cephalopods*, and *captacula* of *scaphopods*; cf. *caducous*.

- axial:** in gastropods, used for sculpture that is more or less parallel to the coiling axis.
- axoneme:** microtubular structure sheathed by a membrane that is continuous with the cell, or plasma membrane; forms core of **cilium** or **flagellum**; comprises two single microtubules, surrounded by nine double microtubules.
- bacteriocyte:** cell containing symbiotic bacteria.
- Bajocian:** lowermost stage of the Middle Jurassic in the European stratigraphic system.
- bathyal zone:** oceanic floor between depths of 200 m and 4000 m.
- bathybenthic:** bottom-dwelling between depths of 200 m and 4000 m.
- bathypelagic:** dwelling in water column between depths of 1000–4000 m.
- beak:** pointed dorsal angle of valve, including the larval shell or **prodissoconch**; mandibles of cephalopod.
- Bernard/Munier-Chalmas hinge notation:** notation system for heterodont hinge teeth based on their ontogenetic development.
- biconical:** shape formed by two cones placed base to base.
- billabong:** a small water body remaining in the dry season, as: pools after the main channel dries up (channel billabong); damming of a tributary mouth by levee of main stream (backflow billabong); remnant secondary channel, an oxbow or a depression on the floodplain (floodplain billabong).
- bioluminescent counter-shading:** production of downward directed bioluminescent light at the same intensity as the down-welling light from the surface, to disrupt or remove an animal's silhouette.
- biostratigraphy:** stratigraphy based on palaeontological aspects of rocks.
- bioturbation:** mixing of sediment by burrowing, feeding or other activities of animals.
- bipectinate:** refers to **ctenidia** bearing two rows of gill leaflets.
- blade:** radial, inwardly widening partitions of organic matter only secreted by the endosiphuncular epithelium in endoceridan nautiloids.
- blastomere:** cell formed during initial division of fertilised egg.
- blastula:** early embryonic stage comprising a hollow sphere of cells.
- blood gland:** follicular gland mass on anterior aorta in several opisthobranch groups; possibly associated with amoebocyte production.
- body whorl:** see **last whorl**.
- bolsters:** formed of anastomosed muscle fibres and connective tissue, or cartilage-like material; support the radular structure in monoplacophorans, polyplacophorans and scaphopods.
- boules cells:** primary digestive cells of cephalopods.
- brevicone:** a short, rapidly-widening shell, as in some nautiloids.
- brood pouch:** chamber in which fertilised eggs are retained.
- brooding:** see **ovoviviparity**.
- buccal cones:** eversible structures for holding prey on each side or around the mouth in some gymnosomes.
- buccal glands:** mucous glands in roof of buccal cavity of polyplacophorans and some gastropods; not homologous with the salivary glands.
- buccal mass:** a complex globular structure encircled by arms and tentacles, comprising the principal organs of feeding – **beak**, **radula**, **radular sac**, muscles, supportive cartilages and other components.
- buccal membrane:** thin web of tissue encircling buccal mass; reinforced by muscular buccal supports that link by buccal connectives to arms.
- bullette:** thickened deposit on the inner surface of the **septal neck** of nautiloids; broader and thinner than an **annulus**.
- bulloid:** globular in shape.
- Burdigalian:** Miocene stage in European stratigraphic system, approximately 16–14 million years before present.
- bursa copulatrix:** sperm sac opening to the vagina; serves as the receiving chamber for the penis during copulation and the initial receptacle for **exogenous sperm**.
- bursicle:** a small sensory pocket on the efferent edge of a ctenidial leaflet in vetigastropods.
- byssal drifting:** use of the **byssus** for dispersal purposes through flotation in the late planktonic stage.
- byssal gape:** opening between the margins of the valves for passage of the **byssus**.
- byssal gland:** byssal-secreting organ in the bivalve foot.
- byssal groove:** transfers adhesive fluid along the foot from **byssal gland** to the substrate.
- byssal notch:** depression in bivalve shell for passage of **byssus**.
- byssus:** cluster of proteinaceous threads secreted by bivalve **byssal gland**; assists in larval flotation; secures metamorphosed juveniles to the substrate and is retained in some adults for the same purpose.
- caducous:** pertaining to the process of shedding structures or organs, either regularly, such as leaves or deer antlers, or occasionally, as in some philinid opisthobranchs; *cf.* **autotomy**.
- caecum:** the blind end of a duct or cavity; the apical chamber in Nautiloidea.
- calcicole, calcicolous:** organism with a preference for, or requiring habitats rich in calcium, usually calcium carbonate.
- calcifuge, calcifugous:** organism with a preference for, or requiring habitats poor in calcium, usually calcium carbonate.
- calcite:** rhombohedral crystalline form of calcium carbonate, differing in crystalline structure from, and dimorphic with **aragonite**.
- callum:** secondary calcareous structure secreted over pedal gape in some Pholadidae.
- callus:** thickened, often external, shelly layer secreted by the mantle in gastropods; calcareous deposit in umbilicus of nautilids; apical feature in gadilimorph scaphopods.
- Calvin-Benson cycle:** biochemical carbon fixation cycle in chloroplasts, in which carbon dioxide is incorporated into ribulose 1,5-biphosphate, subsequently to form sucrose.

GLOSSARY

- camera:** space or chamber, excluding the endosiphuncle, enclosed between two adjacent **septa** in nautiloids.
- cameral deposits:** calcareous deposits secreted on original **cameral** wall during life of nautiloids.
- Canadian:** series representing the Lower Ordovician in the North American stratigraphic system; includes, from lowest to highest, the **Gasconadian**, **Demingian**, **Jeffersonian** and **Cassinian** stages.
- canal:** a narrow channel or tubular extension of the aperture in gastropods; an **anterior** (or **siphonal**) **canal** is present in most advanced Gastropoda, a **posterior canal** is less common.
- capsule gland:** the distal portion, relative to the gonad, of the **pallial oviduct** of gastropods; produces a thin capsule or membrane around each egg; capsules are linked by **chalazae** of the same material in heterobranchs; see also **albumen gland** and **mucous gland**.
- captacula:** extensible, cerebrally innervated, ciliated filaments used by scaphopods to locate and capture food; originate on a **captacular shield** on each side of buccal tube.
- captacular shield:** see **captacula**.
- capuliform:** with the form of a depressed cone, slightly coiled and eccentric apically, as in *Capulus*.
- cardinal area:** a flat or slightly concave surface, often triangular in shape, between **beaks** and hinge in some bivalves, wholly or partly occupied by the **ligament**.
- cardinal tooth:** **hinge tooth** in heterodont bivalves that radiates from the beak; see **hinge teeth**.
- carina(e), carinate:** keel(s), keeled; applied to a narrow ridge on body or shell.
- carrefour:** region in pulmonates where the ducts from the spermoviduct, albumen gland, talon and hermaphroditic gland meet.
- caruncle:** elevated ridge or lobe, with presumed sensory function, between or close to rhinophores in some nudibranchs.
- Cassinian:** uppermost stage in the Lower Ordovician (**Canadian** series) of the North American stratigraphic system; equivalent time period to upper **Arenigian**.
- catachomata:** see **chomata**.
- caudal gland:** on the tip of the tail of pulmonates and commonly surmounted by a horn; produces extra mucus associated with locomotion, feeding or reproductive activity.
- Cenomanian:** the lowermost stage in the Upper Cretaceous on the international stratigraphic scale (Middle Cretaceous of some authors).
- central tooth:** = **cardinal tooth** in bivalves; central tooth in radular row (= **rachidian tooth**).
- cephalic lappets:** small flaps of tissue on the sides of the head.
- cephalic shield:** structure covering the head of cephalaspideans, often with a shallow groove along the midline and a pair of rounded flaps; adaptation for epifaunal burrowing; also in pulmonate family Athoracophoridae; = **head shield**.
- cephalic tentacles:** paired, sensory, horn-like projections on the head directed antero-dorsally, each typically bearing an eye, in 'prosobranchs' and pulmonates.
- cephaloconi:** adhesive **buccal cones** of the gymnosome family Notobranchaeidae.
- cephalocyst:** accommodates the albumen sac in pulmonate embryo; regresses before hatching.
- cephalopedal sinus:** drains venous blood from the head and foot in gastropods.
- cephalopodium:** anterior part of cephalopod, comprising the head, circumoral appendages and **funnel**; see also **visceropallium**.
- cercaria(e):** infective larva(e) of digenetic trematode produced asexually from a **redia** within the molluscan host.
- cerata:** clustered tubular outgrowths along both sides of the body, in nudibranchs and some sacoglossans; each **ceras** acts as a gill and contains a terminal branch of **digestive gland** in the Aeolidina.
- cerebral gland:** neurosecretory centre closely associated with cerebral ganglion of pulmonates.
- cerebrobuccal ring:** simple nerve ring encircling the buccal tube of polyplacophorans.
- chalazae:** string-like links between egg capsules formed of capsule material in heterobranchs; see **capsule gland**.
- Chazyian:** lowermost stage of the Middle Ordovician in the North American stratigraphic system; above the **Canadian** series.
- chemotaxis:** movement in a certain direction in response to a chemical agent.
- chevron groove:** part of cardinal area for ligament insertion in some pteriomorphs.
- chomata:** small tubercles or ridges and corresponding pits, on internal facing margins of pteriomorphs, typically present close to the hinge, but extending around margins in some species. Those on right valve are termed **catachomata**, those on left **anachomata**.
- chondrophore:** a spoon-shaped, projecting form of **resilifer**; marks attachment of internal layer of **ligament** in bivalves.
- chromatophore:** small, thin-walled, elastic sac containing pigment in cephalopod integument; contraction of attached radiating muscle fibres produces rapid colour changes.
- ciliary creeping:** beating of cilia in the mucus under the sole to propel the body; = **ciliary locomotion** in molluscan terms.
- ciliary locomotion:** see **ciliary creeping**.
- cilium, cilia:** fine, hair-like organelle(s) up to 10 µm long and 0.5 µm in diameter, comprising an **axoneme** attached to a basal body; beats with a lash-like stroke; see also **flagellum**.
- circum-anal gills:** circle of secondary gills on the posterior midline surrounding the anus of dorid nudibranchs.
- circum-oesophageal ring:** formed of the paired cerebral, pleural and pedal ganglia, to which the visceral and parietal ganglia are linked, in gastropods.
- cirri:** thin, tendril-like, tactile appendages on the arms of cirrate octopods and *Vampyroteuthis*; alternate with suckers.
- clade:** a taxonomic group consisting of an ancestral taxon and its descendants.
- cladohepatic:** branched state of the **digestive gland** internally in some opisthobranchs; converse is **holohepatic**.
- clathrate:** latticework of **spiral** and **transverse** (axial) ornamentation intersecting more or less at right angles.
- clavus:** see **club**.

cleioproctic: anus opening to the exterior among the cerata behind the **inter-hepatic space**; used previously in superfamilial division of Aeolidina; see also **acleioproctic** and **pleuroproctic**.

club, also **clavus**: terminal expansion of the rhinophore, formed of lamellae or papillae, in all nudibranchs.

cnidosac: a sac at the ceratal tips of Aeolidina containing functional cnidarian stinging cells (nematocysts) removed from cnidarians during feeding.

coelom: body cavity formed within, and lined with mesoderm; comprises renal, pericardial and gonadal cavities; restricted to the posterior pericardium and possibly upper gonoduct in Aplacophora.

coelomic gonoduct: mesodermal component of the reproductive system.

coelomoduct: tubule, derived from coelomic tissue, connecting the **coelom** with the external environment.

collabral: parallel to the outer lip, the most common form of sculpture in gastropods. A more precise term than 'axial'. Collabral sculpture may be **prosocline**, **orthocline** or **opisthocline**.

collostyle, a rod of connective tissue that fills the centre of radular gland.

columella: the pillar forming the central axis of a gastropod shell around which the whorls spiral.

columellar lip: = inner lip.

columellar muscles: attachment of the body to the shell in gastropods; originate on **columella** and insert in the head and foot; retract/extend the head and foot in/out of the shell or **last whorl**; single in higher vetigastropods and caenogastropods, paired in others; homologous with **shell muscles**.

commarginal: with reference to structure reflecting the former shell margin, especially in bivalves, also in gastropods; equivalent to concentric.

commissure: a band of neural tissue linking two sides of the nervous system or two neural centres (ganglia); the line where the two valves of a bivalve meet.

compressed: flattened laterally.

conch: see **shell**.

conchiolin: (= conchin) proteinaceous component of shell, similar to arthropod chitin.

conspiral: shells in which the spire projects as a cone.

connecting ring: structure linking **septal neck** with next most posterior **septum** in shell of nautiloids.

consecutive hermaphroditism: widespread form of hermaphroditism, in which the individual changes, usually once, from male to female (**protandry**) or much less often from female to male (**protogyny**).

conus: hollow, conical structure at posterior end of gladius.

convolute: coiling in gastropods and nautiloids in which the **last whorl** completely envelops the previous whorls.

corbiculoid: (= cyrenoid) **dentition**: **heterodont** hinge dentition with three cardinal teeth on each valve.

cord: coarse rounded linear sculpture, spiral or transverse, on the shell surface; less prominent than **costa** or **rib**.

cornea: transparent covering over the eyes of Loliginidae.

costa: rib-like rounded ridge on the surface of a shell; rib used much more commonly.

cratonic: a stable part of the continental crust that has been little deformed for a long period.

crenulated: finely notched or corrugated, as in the edge or margin of a shell.

crista: moderately broad, prominent ridge on shell surface.

crop: an expansion of the oesophagus forming an ancillary structure to the stomach.

crop juice: mixture of digestive enzymes for digestion of carbohydrates, proteins and lipids.

cruciform: in the form of a cross.

crus (crura): narrow ridge, tooth, nodule or elevated area on the interior of some pteriomorphs (mainly Pectinoidea and Anomioidea); termed **cardinal crus** when situated near the ligament pit, and **auricular crus** when at the base of an auricle.

cryptobranch: pertaining to gills that can be withdrawn into a pocket (thus hidden or discreet), as in eudoridoidean opisthobranchs; converse of **phanerobranch**.

crystal sac: passes particles retrieved from faecal material to the **capsule gland** for external covering of egg capsules in Neritoidea; = **reinforcement sac**.

crystalline style: organ of extracellular digestion; releases amylase and other enzymes incorporated within it; formed in style sac of some gastropods and most bivalves and projects into the stomach.

ctenidium, ctenidia: homologous respiratory organ(s), or gill(s), in the mantle cavity of bivalves, many gastropods, cephalopods, monoplacophorans and aplacophorans, and in pallial groove of polyplacophorans; each comprises an axis carrying right and left series of lamellae or gill leaflets. Ctenidia bearing one or two rows of leaflets are **monopectinate** or **bipectinate**, respectively; dual roles in respiration and food filtering to different degrees in bivalves and a few gastropods; see also **demibranch** and **gill**.

ctenodont: form of **taxodont** hinge with numerous teeth transverse to margin.

ctenolium: row of small teeth resembling a comb on ventral side of **byssal notch** in some Pectinoidea.

cuspidate: sharply pointed.

cyrtocone: nautiloid shell that curves less than a full circle.

dart sac: muscular caecum in the vagina of helicoidean pulmonates; stores 'love darts' delivered by the dart apparatus during the mating ritual.

deciduous: pertaining to structures easily autotomised, or shed by the animal as a defensive reaction.

decollate: shedding of apical **whorls** in some gastropod groups; shell may be sealed with a septum.

decussate: diagonally reticulate or netlike sculpture in gastropods formed by intersection of **prosocline** and **opisthocline** elements.

demibranch: one of a pair forming each **ctenidium** of bivalves, each comprising a descending and an ascending lamella.

Demingian: stage in lower Middle **Canadian** series of the Lower Ordovician in the North American stratigraphic system; equivalent time period to uppermost part of Tremadocian stage.

GLOSSARY

dendritic 'gills': a set of highly branched tubular structures, used for respiration, along the edge of the **dorsum** in the *Dendronotina*.

depressed: flattened dorso-ventrally.

desmodont: hinge dentition in members of *Myoida*; small or no **cardinal teeth** and no **lateral teeth**; accessory ridges may replace the teeth along the hinge line.

detorsion: shown by many opisthobranchs and pulmonates, in which the effects of **torsion** have been reversed to some degree.

deviated: of the gastropod **protoconch**, where the coiling axis is oblique to that of the **teleoconch**.

dialyneury: the fusion of the nerves of two ganglia.

diaphragm: a fibrous 'wall' separating the organs of the head cavity and the viscera within the visceral hump in *Aglaidae*.

diastole: the relaxation and dilation phase of a heart beat, particularly of the ventricle.

diaulic: reproductive system in which the gonoduct has two openings to the exterior.

digestive diverticula: major lobes of **digestive gland**.

digestive gland: simple to complex organ linked by duct(s) or opening directly to stomach; undertakes extracellular (aplacophorans, polyplacophorans, cephalopods) or intracellular digestion (bivalves) or both (gastropods, scaphopods), and absorption of digestive products and storage of reserves in advanced groups; also involved in some excretion; may be termed **liver**; see also **midgut gland**.

digestive tubules: components of the **digestive gland**.

dimyarian: see **adductor muscles**.

dioecious: individuals are male or female throughout life.

diotocardian: heart formed of a single ventricle and two auricles.

direct development: all larval development occurs in the egg capsule, from which a small benthic version of the adult hatches; see also **planktotrophic** and **lecithotrophic** development.

discoblastula: product of bilaterally symmetrical **meroblastic** cleavage forming a disc of cells on top of a large, uncleaved yolk mass; among molluscs only occurs in cephalopods.

dissoconch: post-larval bivalve shell.

distichous radula: comprises two teeth per row; in aplacophorans.

ditaxic: pedal wave form, in which locomotory waves traverse the foot as two system of waves, one each side of the mid-line; compare **monotaxic** and **tetrataxic**.

ditrematous: separate male and female genital openings; in pulmonates.

divaricate: sculpture comprising widely diverging linear ridges.

docoglossate radula: two or three hardened, robust teeth in each row; typical of *Patellogastropoda*.

dorsal bodies: neurosecretory centres associated with pulmonate cerebral ganglion.

dorsum: in cowries (*Cypraeoidea* and *Triviidae*) the convex part of the shell opposite the aperture; the back of shell-less opisthobranchs, homologous with the mantle of shelled forms; sometimes used when derivation of dorsal tissues is uncertain.

ductus enigmaticus: a third reproductive duct in some *trialeulic* neritids that is thought to carry waste to the mantle cavity.

duplivincular ligament: lamellar component of **ligament** divided into bands, each cross-linking the cardinal areas of the two valves.

dwarf males: extreme form of dimorphism in which males are minute and live attached to or within the female.

dysodont: hinge dentition with a few small, simple and seemingly ineffective teeth close to the beak.

dystenoid: configuration of nervous system in *Viviparidae*, in which the pleural ganglia are associated equally with the cerebral and pedal ganglia (compare **hypathroid** and **epiathroid**).

eave: overhanging lateral **tegmental** edge of the **intermediate plate** of polyplacophorans.

echinospira larva: characterised by a secondary larval shell or **scaphoconch** that assists in flotation; in mesogastropod families *Lamellariidae*, *Velutinidae*, *Triviidae*, *Eratoidea* and *Capulidae*.

ect-aquasperm: see **aquasperm**.

ectoderm: the outermost layer of germ cells developed during gastrulation.

ectosiphuncle: outer sheath of **siphuncle**, composed of successive **connecting rings** and **septal necks** in nautiloid shell.

edentulous: lacking hinge teeth.

efferent membrane: links the ventral surface of the ctenidial axis with the mantle skirt and carries the efferent branchial vessels taking blood to the **atrium** of the heart.

egg capsule: usually lens-shaped, covered with sand grains or horny; see also **ootheca**.

egg gland: = **capsule gland**.

ejaculatory duct: a muscular internal duct carrying sperm to the penis, or within the base of the penis, in some gastropods.

elasmognathous: plate-like.

eleutherorhabdic: form of gill in which adjacent filaments adhere by discs or patches of cilia only.

emarginate: bluntly notched along a margin.

Emsian: uppermost stage of Lower Devonian in international system; below Eifelian stage of Middle Devonian.

endobyssate: infaunal attachment within substratum using a mesh of byssal threads.

endocone, endoconic: one of, or pertaining to, a series of calcareous cones formed in **adapical** portion of **siphuncle**; usually in endoceridan or discosoridan nautiloids.

endoderm: the innermost layer of germ cells developed during gastrulation.

endogenous sperm: self-produced sperm; converse of **exogenous sperm**.

endolithic: living within rock.

endsiphocone: conical space inside most recent endocone in endoceridan or discosoridan nautiloid shell.

endosiphotube, endosiphuncular tube: tube connecting apices of endocones in some endoceridan nautiloids.

endosiphuncle: space within **ectosiphuncle**, including organic tissues and calcareous structure.

endostyle: a glandular area on the ctenidial axis that produces a feeding web of mucus in some filter-feeding gastropods.

endosymbiont: symbiont that lives within another organism; usually restricted to associations that are mutually beneficial.

ent-aquasperm: see **aquasperm**.

epiathroid: a condition of the nervous system in which the connectives between the pleural and pedal ganglia are long, and those between pleural and ventral ganglia are short (converse of **hypoathroid**).

epibenthos, epibenthic: organisms living on the seabed or lake floor.

epiboly: gastrulation process in which presumptive ectoderm grows over and envelops the presumptive endoderm.

epibyssate: bivalves that attach to the surface of hard substrata by a byssus.

epifauna: all animals living on the surface of the substratum.

epipelagic: pertaining to the upper ocean to a depth of 200 m.

epiphallus: non-eversible muscular expansion of the **vas deferens** in pulmonates that enters the penis through a simple pore or elaborate **verge**; important in **spermatophore** formation.

epiphragm: a mucous shield secreted across the **aperture** by some terrestrial pulmonates that reduces moisture loss while still being permeable to oxygen; may be partially calcified; usually associated with **aestivation**.

epiphytic: pertains to organisms living on the surface of a plant.

epiplankton: plankton living in the top 200 m of the ocean.

epipodium: muscular expansion of the lateral and upper surfaces of the foot, that forms the **parapodia** or **wings** of opisthobranchs, or bears various features, such as cephalic lappets, **neck lobes**, and sensory areas, tentacles, papillae and micropapillae in some other gastropods, notably vetigastropods.

epiproboscis: a conspicuous, protrusible, buccal structure in the Mitridae bearing the salivary ducts; possibly an adaptation for feeding on soft-bodied, reclusive prey.

epipsammic browsing: use of the radula to remove micro-organisms adhering to sand grains taken into the buccal cavity.

epistellar bodies: photosensitive vesicles on the stellate ganglion in the mantle of octopods or close to the optic tract of decapod cephalopods; may monitor down-welling light.

equilateral: **umbo** located midway between the anteriormost and posteriormost portions of the shell in bivalves.

equivalve: valves in bivalves equal in size and form.

escutcheon: differentiated area on a bivalve extending posteriorly from the beak.

eulamellibranch: symmetrical, W-shaped ctenidial form, with connected filaments; in heterodonts and some anomalodesmatans.

eupyrene spermatozoa: = **euspermatozoa**.

euryhaline: tolerant of a wide range of salinities; converse **stenohaline**.

eurysiphonate: term applied to nautiloids with a relative large siphuncle.

euspermatozoa: haploid spermatozoa that fertilise the eggs; one of two types of spermatozoa in 'prosobranchs'; see also **paraspermatozoa**.

euthyneury: simple loop-like form of gastropod visceral nerves, following partial or complete **detorsion**.

evolute: coiling in gastropods and nautiloids in which the whorls are not in contact or are barely touching.

excurrent siphon: = **exhalant siphon**.

exhalant siphon: tubular orifice through which exhalant water is expelled; formed by the posterior end of the mantle in 'prosobranchs', inner mantle fold in fissurellids, and by posterior fusion of mantle margin in bivalves.

exogenous sperm: received from a partner during copulation; generally received in **bursa copulatrix** and stored in **seminal receptacle** until required for fertilisation; converse of **endogenous sperm**.

external fertilisation: characteristic of broadcast spawning, where fertilisation occurs during mixing of gametes in the water column.

extrapigmental ocellus: **megalaesthete** pigmented terminally, with retina-like cells beneath a **tegmental lens**.

fertilisation chamber/area: at the distal end of the **upper oviduct** in caenogastropods, or **hermaphroditic duct** in opisthobranchs and pulmonates; generally near opening of **seminal receptacle**.

filibranch: symmetrical, W-shaped ctenidial form, with loosely connected filaments; in many pteriomorphs.

fimbriate: fringed.

flagellum: fine, hair-like organelle similar in structure to a **cilium**; 15–30 µm long, comprising an **axoneme** attached to a basal body; beats with an undulating rhythm; see also **cilium**.

flammulate: flame-like.

flank: central part of valve surface of bivalves.

flexoglossate: radula type associated with a curved odontophoral bending plane, allowing lateral splaying of the radula at its most functional point; provides for functional diversity; compare **stereoglossate**.

food channel: a mid-dorsal groove between two epithelial folds in the posterior buccal cavity and anterior oesophagus in 'prosobranchs'.

food groove: a groove on the edge of demibranchs of bivalves or in the pallial cavity and on the neck of filter-feeding gastropods.

food string: a string of mucus, bearing trapped food particles, rotated by **style**; winds through the stomach, over the ciliary sorting area, and protrudes into the intestine.

foot: the large muscle mass on which gastropods and polyplacophorans move, comprising the pedal sole, subdivided into an anterior **propodium** and a posterior **metapodium**, and the pedal rim or **hyponotum** (see also **mesopodium**, **epipodium**, **parapodia**, **footlobes**); separated from **girdle** by **pallial grooves** in polyplacophorans; laterally compressed in bivalves and used by most species for burrowing, but reduced in size and used for mantle cleaning and/or byssal secretion in many Pterioidea; a narrow burrowing organ in scaphopods, similar to that of bivalves; subdivided into arms in cephalopods; non-muscular, ciliated fold in ventral groove of neomenioids, used for ciliary locomotion.

GLOSSARY

- footlobes:** structures between the **wings** of Gymnosomata; considered to be homologous with the foot in other molluscs.
- fossette:** a small pit, depression or socket.
- fossula:** in cowries, a shallow groove or depression on the abapical part of the inner lip, bordered by a narrow ridge.
- foveola:** transverse membranous fold of skin forming a pocket in the funnel groove of some ommastrephid squids.
- funicle:** a narrow ridge of **callus** spiralling into the umbilicus of a gastropod shell.
- funnel:** exhalant respiratory and locomotory tube of cephalopods; mobile and directional in coleoids and involved in jet propulsion.
- funnel locking apparatus:** three interlocking pairs of cartilages linking the **cephalopodium** and **visceropallium** of decapod cephalopods; comprises the dorsal and two latero-ventral pairs of **mantle cartilages** and **funnel cartilages**.
- funnel cartilage:** see **funnel locking apparatus** in cephalopods.
- fusiform:** spindle-shaped.
- gametoduct:** duct carrying gametes from the pericardium to the mantle cavity in Aplacophora.
- gametolytic gland:** = **bursa copulatrix**.
- gametolytic sac:** = **bursa copulatrix** in opisthobranchs.
- gape:** opening remaining between the closed **valves** of a bivalve, usually for passage of **siphons**, **foot** or **byssus**.
- Gasconadian:** lowermost stage in the Lower Ordovician, and of the **Canadian** series, in the North American stratigraphic system; equivalent time period to the lowermost part of the Tremadocian stage.
- gastric caecum:** posterior portion of molluscan stomach typically used as a sorting area.
- gastric shield:** a heavily cuticularised area of the dorsal or postero-dorsal gastric epithelium, on which the **style** is rotated; **gastric shield** of chaetoderms considered analogous to that in other molluscs.
- gastrulation:** formation of the embryonic **ectoderm**, **mesoderm** and **endoderm** layers.
- genus-group:** includes all taxa at the ranks of genus and subgenus.
- geosyncline:** a large-scale (20+ km), elongate, mobile down-warping of the earth's crust.
- gill:** applied to a wide variety of respiratory structures, including **ctenidia**; see also **secondary gills**.
- girdle:** muscular, sometimes fleshy, structure supporting **valves** or **plates** of polyplacophorans.
- gizzard:** a modified region of the gut used for masticating food.
- gladius:** thin, chitinous, feather-shaped remnant of the shell in teuthoids and some sepioids.
- gland of Leiblein:** extrinsic gland connected to the oesophagus of neogastropods by a narrow duct; derived from the **oesophageal gland**; terminal bulb of poison gland of toxoglossans also homologous.
- glochidia:** larvae of fresh water unionoidean bivalves brooded between gill lamellae; adapted to parasitise the gills of fish.
- gonochoristic:** = **dioecious**.
- gonoduct:** duct carrying sperm or ova from the gonad to the exterior.
- gonopericardial duct:** transfers gametes from gonad to pericardium in aplacophorans.
- grade:** a taxon consisting of independent lineages and based on non-homologous or plesiomorphic characters.
- graptolite:** a colonial marine organism (Class Graptolithina) with organic cup-shaped or tubular exoskeleton; tentatively assigned to Cnidaria or Hemichordata.
- gynandry:** see **consecutive hermaphroditism**.
- hadal:** oceanic depths exceeding 6000 m.
- haemocoel:** a blood-filled body cavity.
- haemocyanin:** respiratory pigment containing copper in the haemolymph of many molluscs, especially gastropods and cephalopods.
- haemocytes:** see **amoebocytes**.
- haemoglobin:** intracellular or extracellular respiratory pigment containing iron present in blood plasma of some gastropods and bivalves in poorly oxygenated habitats.
- haemolymph:** fluid in circulatory system of numerous invertebrate groups.
- haliotiform:** ear-shaped, as in the shell of Haliotidae.
- hamulus:** hook-like process.
- Hancock's organs:** paired chemoreceptors usually in the groove between the foot and the **cephalic shield** in cephalaspideans.
- head shield:** see **cephalic shield**.
- head valve:** anterior shell plate of polyplacophorans.
- head-foot:** the lower and largely muscular part of the gastropod body associated with the external environment, movement and feeding; can be withdrawn within the **last whorl** in shelled gastropods.
- heart:** comprises a **ventricle** and paired **auricles** within the **pericardium**, except in many gastropods that have a single auricle, and in *Nautilus* and monoplacophorans that have two pairs of auricles; rudimentary in scaphopods; see **monotocardian**, **diotocardian**.
- hectocotylus:** modified tip of one or two arms of male coleoid cephalopods; used for transfer of spermatophores from the penis to the seminal receptacle of the female; see also **spadix**.
- helicocone:** shape of shell as a coiled tube that expands distally.
- hermaphroditic duct:** links **ovotestis** and point of division between male and female ducts in opisthobranchs or the pulmonate **carrefour**; may include an **ampulla** or **seminal vesicle**; equivalent to visceral **vas deferens** and **coelomic gonoduct**; also termed **spermoviduct**.
- hermaphroditism:** **consecutive** or **simultaneous** function of male and female sex organs in the same individual.
- heterochrony:** different rates of development of one or more features in two or more ontogenies; see also **paedomorphosis**.
- heterodont:** hinge dentition with upright **central** or **cardinal teeth** below the **beak** and usually with elongate **lateral teeth** on each side of the **beak**; **lucinoid** and **corbiculoid** arrangements are two main forms.

heteromyarian: see **adductor muscles**.

heterorhabdic: ctenidial filaments comprise larger ones at the inner base of the folds and smaller ones elsewhere.

heterostrophic: coiling in opposite directions, for example, the **protoconch** and **teleoconch**.

hibernation: state of dormancy or torpor undergone by some animals in cold periods; analogous to **aestivation**.

hinge plate: calcareous platform internal to **beak**, bearing **hinge teeth**.

hinge teeth: projections on dorsal margin of **valve**; interlock and align closed valves; anterior **lateral** and **cardinal teeth** develop from anterior **lamellae**; posterior **lateral teeth** develop from posterior **lamellae**.

holoblastic: early embryonic cleavage pattern in which cell membranes divide cytoplasm and yolk completely; in forms with a small volume of yolk; compare **meroblastic**.

holobranchial: **gills** (= **ctenidia**) present along entire pallial groove of Polyplacophora; compare with **merobranchial**.

holocrine glands: produce secretion comprising dissolved cells and their products.

holohepatic: discrete, unbranched internal state of the digestive gland in some opisthobranchs; converse is **cladohepatic**.

holopelagic: pelagic organisms that spend their entire lives in the water column; compare **meropelagic**.

holophyletic: = **monophyletic**: sharing a common ancestor.

holoplankton: planktonic organisms that remain in the water column throughout their entire life; compare **meroplankton**.

holopodous: pedal grooves are inconspicuous or close to the angle of the foot in pulmonates; see also **aulacopodous**.

homeostrophic: the **protoconch** and **teleoconch** coil in the same direction.

homomyarian: see **adductor muscles**.

homoplasy: correspondence in morphology of different organisms as a result of evolutionary convergence or parallel evolution.

homorhabdic: ctenidial filaments are all alike, in bivalves.

hook sac: eversible sac on each side of the **radula** in gymnosomes, containing numerous chitinous hooks; used in feeding.

hull: extracellular elaborate coating around, and largely formed by the oocyte of polyplacophorans.

hydrostatic skeleton: controlled support provided by muscular pressure on body fluids, especially the major venous sinuses; used to modify body or organ shape.

hyperpyrene spermatozoa: see **paraspermatozoa**.

hypoathroid: a condition of the nervous system in which the pleural and pedal ganglia are adjacent, the connectives between them are short, and connectives between pleural and cerebral ganglia are long (converse of **epiathroid**).

hypobranchial gland: paired glands (single in many gastropods), comprising glandular columnar epithelium on the mantle roof; produce secretion that consolidates sediment from inhaled water for rejection.

hypodermic insemination: injection of sperm into partner through the body wall by some opisthobranchs.

hyponomic sinus: large concave sinus in the aperture, marking the ventral midline of nautiloid shell.

hyponotum: the outer pedal rim of the foot of systellomatophoran pulmonates; see also **notum**.

hyporheos: the interstitial fauna of the **hyporheic zone**, the region between true groundwater beneath and the stream above.

hypoplax: elongate accessory plate along postero-ventral margin of valves in some Pholadidae.

hypostracum: innermost layer of **valve** in polyplacophorans; composed of columnar crystals lining the ventral surface of each valve.

hystricoglossate radula: a specialised form of the rhipidoglossate type found in Pleurotomariidae.

imbricate: overlapping or shingle-like.

imperforate: shell lacks an umbilicus.

imposex: the appearance of male reproductive parts, including a penis and/or a vas deferens, in females of dioecious gastropod species.

incirrate: octopod cephalopods lacking **cirri** on the arms.

incurrent siphon: see **inhalant siphon**.

inequilateral: **beak** located noticeably closer to anterior or posterior end of **valve** in bivalves; converse is **equilateral**.

inequivalve: valves unequal in size and form in bivalves.

infauna: benthic animals living within the substratum.

infrabranchial chamber: portion of mantle cavity of bivalves ventral to the **ctenidia**.

infula: double-walled organic layer encircling part of **endocone** deposit in endoceridan nautiloids; contained small spaces and tubes with organic walls lying in longitudinal grooves in the completed deposit.

ingesting gland: usually considered to digest excess sperm; present between the **albumen gland** and the **capsule gland**.

inhalant siphon: a tubular fold in the mantle – anteriorly in caenogastropods and a few bivalves, posteriorly in most bivalves – through which inhalant water is drawn.

inner fold: see mantle folds.

inner lip: inner margin of aperture overlying columella including parietal wall.

insertion plates: lateral extensions of the **articulamentum** in polyplacophorans; usually divided into **insertion teeth** by slits.

insertion teeth: see **insertion plates**.

inter-hepatic space: the gap between the anterior or pre-pericardial ceratal groups and the posterior or post-pericardial ceratal groups in some nudibranchs.

intercalary: inserted between original components.

intermediate valves: shell plates of polyplacophorans between the **head valve** and **tail valve**.

internal fertilisation: transfer of spermatozoa, sometimes in a **spermatophore**, by one male to one female, usually through copulation; see also **pseudocopulation**.

GLOSSARY

- interspace:** space in polyplacophorans between the posterior ends of left and right gill rows that do not meet around the anus; groove or gap between spiral or axial **ribs** in shell sculpture.
- intraembolic proboscis:** comprises the buccal mass as its base and an oral tube that can elongate; typical of Conoidea.
- intrapigmental ocellus:** polyplacophoran **megalaesthete** with subsurface pigment cup coupled with a few retinal cells and a small lens.
- intritacalx:** a calcareous, chalky outer layer on some gastropods, apparently homologous with the **periostracum**, and typically finely and intricately sculptured.
- introsperm:** sperm of forms with internal fertilisation.
- involute:** coiling in which the **last whorl** of a gastropod or nautiloid almost completely envelops the previous whorls, leaving only a little of the latter exposed in the umbilicus.
- iridophores:** iridescent cells in the surface epithelium of heteropods and some opisthobranchs.
- isodont:** hinge dentition with large, subequal, symmetrically placed teeth.
- isomyarian:** see **adductor muscle**.
- iteroparity:** breeding in more than one season, often at regular intervals.
- Jeffersonian:** upper Middle **Canadian** series of the Lower Ordovician in the North American stratigraphic system; equivalent time period to lower **Arenigian**.
- jelly gland:** a distal gland in the pallial oviduct of Littorininae.
- jugum:** the longitudinal median ridge of intermediate, and of some posterior, valves of polyplacophorans.
- K-selection:** competitive ability in stable conditions; population stays close to the carrying capacity of the habitat; promotes **iteroparity**, moderate life-span, pelagic larvae and potentially wide dispersal; see **r-selection**.
- kidney:** **coelomoduct** with deeply folded walls; excretory and filtration organ commonly linked to the pericardial cavity by a ciliated **renopericardial canal**.
- kleptoplasty:** the retention of live plastids (cellular organelles) from ingested algae by sacoglossans for use of their photosynthetic production.
- labial:** pertaining to the **inner lip** of a gastropod shell, or to the lips of the mouth.
- labial palps:** triangular, ridged appendages on each side of the mouth used by all bivalves and protobranchs to sort food; derived from remnants of larval **velum**.
- labial teeth:** in cowries, the narrow, transverse ridges on the inner margin of the outer lip (*i.e.* used in the opposite sense to 'labial' above).
- labium:** = **inner lip** of gastropod shell.
- labral:** pertaining to the **outer lip** of gastropod shell.
- labral teeth:** in cowries, the transverse ridges on the inner or columellar lip (*i.e.* used in the opposite sense to 'labral' above). The term 'columellar teeth' is preferable.
- labrum:** = **outer lip** of gastropod shell.
- lamel:** thin plate-like component of shell microstructure in most heterodonts, deposited parallel with the shell surface; often rectangular, and comprising **lamellae**.
- lamellae:** thin plate-like structures.
- lamellar layer:** see **ligament**.
- lanceolate:** spear-shaped.
- lappets:** muscular extensions of the **buccal membrane** of sepoid and teuthoid cephalopods; additional folds associated with the mouth.
- Larapintine Sea:** a well-defined, narrow sea that extended across north-western Western Australia and southern Northern Territory in the mid-Ordovician period.
- larviparity:** brooding of young to, or nearly to, pediveliger stage before release, followed by settlement and metamorphosis.
- last whorl:** the last, most recently formed whorl of a gastropod; term preferred to **body whorl**.
- lateral area:** triangular area on the tegmentum of intermediate polyplacophoran valves, on each side of the jugum and posterior to the pleural area.
- lateral tooth:** see **radular teeth, hinge teeth**.
- latero-marginal teeth:** see **radular teeth**.
- lecithotrophic:** form of development in which larvae generally do not feed, relying on yolk in egg, and briefly are planktonic before settlement and metamorphosis; (Greek: *lecith* = yolk, *trophos* = one who feeds); see also **planktotrophic** and **direct development**.
- lentic:** pertaining to still, calm or slow-moving water, such as lakes.
- lenticular:** lens-shaped, convex on one or more surfaces.
- licker:** see **subradular organ**.
- ligament:** horny, elastic, dorsal structure in bivalves that joins and opens valves when adductor muscles relax; formed of internal fibrous and an external non-fibrous or **lamellar layer**; **amphidetic** ligaments extend anterior and posterior to the beak; those only attached posterior to the beak are **opisthodetic**.
- light organs:** see **photophores**.
- limacisation:** the process of morphological and physiological change associated with the evolution of a slug-like form in pulmonates.
- lipofuscin:** a lipid pigment.
- lirae, lirate:** sculpture of fine ridges or lines on surface of shell.
- lithodesma:** small calcareous plate reinforcing the ligament in some bivalves.
- liver:** applied to **digestive gland**.
- longicone:** elongate, tapering shell, as in some nautiloids.
- lotic:** of fast-flowing water bodies, such as streams and rivers.
- love dart:** = *telum amoris*; a calcareous needle produced in the **dart sac**; darts exchanged by mating helicoideans stimulate courtship behaviour.
- lucinoid:** form of **heterodont** hinge dentition with two **cardinal teeth** on each valve.
- lunule:** depression anterior to the **beak** of a bivalve.
- lysosomes:** specialised cell organelles containing hydrolytic enzymes.

Maastrichtian: the uppermost stage in the Upper Cretaceous on the international stratigraphic scale.

magnocellular lobes: located each side of the junction of brachio pedal and suboesophageal cords; control centres for giant nerve system of teuthoid cephalopods.

mantle: the integument surrounding the visceral mass of molluscs; secretes the shell where this is present.

mantle cartilage: see funnel locking apparatus.

mantle cavity: invagination under the mantle that accommodates **ctenidia**, **osphradia** and often **hypobranchial glands** in most groups; represented by **pallial grooves** in polyplacophorans and monoplacophorans; space enclosed by the **mantle skirt** of marine gastropods; latero-ventral space surrounding visceral mass in bivalves; see also **nuchal cavity**.

mantle edge: the anterior margin of the mantle in gastropods, that may be thickened to form a collar.

mantle folds: up to three folds or lobes at mantle edge in bivalves; roles of the **inner**, **middle** and **outer folds** are predominantly, but not exclusively, muscular, sensory and secretory.

mantle-line: a distinct line in the shell pattern indicating the edge of the mantle lobes, or where the left and right lobes of the mantle meet, as in Cypraeidae.

mantle locking apparatus: see funnel locking apparatus.

mantle papillae: small processes on **mantle edge**, usually but not always on the **middle fold**; may be light- or chemoreceptors.

mantle skirt: the extended edge of the **dorsum** or the **mantle** in shell-less opisthobranchs; expanded dorsal body wall that encloses the **mantle cavity** in 'prosobranchs' and pulmonates.

marginal plates: plate-like **marginal teeth**; see **radular teeth**.

marginal teeth: see **radular teeth**.

marsupium: part of **ctenidium** of unionoids modified as a brood pouch.

median teeth: see **radular teeth**.

megalaesthete: see **aesthete**.

meiofauna: interstitial animals small enough to pass through a sieve of 1 mm mesh, but are retained by one of 0.1 mm mesh.

membrane gland: = **capsule gland**, a nidamental gland in some opisthobranchs.

mentum: modified propodium (for example, in Pyramidelloidea) forming a snout-like projection beneath the rhynchostome.

meroblastic: embryonic cleavage pattern of zygotes with extensive yolk deposits, in which blastomere cell membranes are incomplete; compare **holoblastic**.

merobranchial: gills confined to the posterior part of the pallial groove of polyplacophorans; converse of **holobranchial**.

méronephridien: caenogastropod renal type in which the primary and secondary lamellae of the renal organ interdigitate; compare **pycnonéphridien**.

meropelagic: pelagic organisms that spend part of their lives in the water column; compare **holopelagic**.

meroplankton: organisms that spend varying lengths of time in the plankton, often during larval stages.

mesoderm: embryonic germ layer in triploblastic phyla; derived from the **endoderm** following **gastrulation**.

mesopelagic: of the oceanic water column beyond the continental shelf, between depths of 200–1000 m.

mesoplax: elongate accessory plate across **umbo** in some Pholadidae.

mesopodium: the central portion of the gastropod foot, applied especially in groups in which it is expanded.

mesurethran: condition in which ureter is short and opens near the side of the kidney; excretory products are released within the pulmonary cavity; compare with **orthurethran**, **sigmurethran**.

metanephridium: multicellular, excretory structure that receives fluids from the coelomic cavity, resorbs non-waste, and discharges waste to the exterior.

metaplast: elongate accessory plate covering postero-dorsal gap between valves in some Pholadidae.

metapodium: the posterior portion of the foot, that bears the operculum when present.

micraesthetes: see **aesthete**.

middle fold: see **mantle folds**.

middle piece, midpiece: region of spermatozoon posterior to the nucleus, containing several mitochondria, the proximal and distal centrioles and the base of the flagellum.

midgut gland: equivalent to **digestive gland** in most molluscs, but comprises anterior **digestive gland** and posterior 'pancreas' of coleoid cephalopods, sometimes termed 'hepatopancreas'.

monaulic system: reproductive morphology in which the ectoderally derived **vas deferens**, **vagina** and **oviduct** share a common duct, but functions are kept separate by grooves and ciliary tracts; see also **diaulic** and **triaulic**.

monoecious: = individuals with both male and female reproductive organs; see **hermaphroditism**.

monomyarian: see **adductor muscles**.

monopectinate: refers to **ctenidia** bearing one row of gill leaflets.

monophyly, monophyletic: comprising an ancestor and all its descendants; see **polyphyly** and **paraphyly**.

monostichous: radula form in aplacophorans, comprising a single tooth per row.

monotaxic: pedal locomotory wave that traverses the foot as a single wave or system of waves; compare **ditaxic** and **tetrataxic**.

monotocardian: heart formed of a single auricle and ventricle.

mucous gland: in general any gland producing mucus; major nidamental gland that produces the characteristic jelly-like egg-masses of opisthobranchs.

mucous string: any strand of mucus; formed by cilia rolling mucus into a string for food collection or waste rejection in the mantle cavity or in the gut.

mucro: a projecting point at posterior end of the jugum on tail valve of some polyplacophorans; point on septum of decollate gastropods.

multifissurate: having numerous slits.

multispiral: with many whorls.

multivincular ligament: comprising serially repeated bands of the alivincular type.

Munier-Chalmas/Bernard hinge notation: notation system for heterodont hinge teeth based on their ontogenetic development.

myophores, myophoric: sites of, or associated with, attachment of muscle.

myostracum: inner prismatic layer of shell underlying muscle attachment areas in Polyplacophora, gastropods and bivalves.

nacre: aragonitic material forming the lustrous, iridescent inner surface or **nacreous layer** of many mollusc shells; may occur as thin, flat sheet nacre, tall, pyramidal columnar nacre, or elongate stack nacre.

nacreous layer: inner calcified layer of shell; composed of horizontal layers of calcite or aragonite crystals between layers of conchiolin.

neck: area immediately posterior to head of gastropods; constricted anterior part of body chamber of nautiloid between aperture and inflated portion; differs from septal neck.

neck flaps: = neck folds or **nuchal lobes:** flaps of tissue on the epipodium that direct inhalant and/or exhalant currents through the mantle cavity.

neck folds: see neck flaps.

nectobenthos: organisms that swim off the floor of the sea or lake.

Needham's sac: elongate, membranous sac that stores spermatophores of coleoid cephalopods after production in the spermatophoric glands.

nekton: free-swimming aquatic animals capable of movement independent of environmental forces, such as currents.

Neocomian: a series in the lower part of the Lower Cretaceous, above the Tithonian-Upper Volgian stage of the Jurassic, and below the Aptian stage.

neoteny: see paedomorphosis.

nephridial gland: highly vascularised part of the left kidney; involved in the transport of ions and small molecules.

nephrolith: spherical concretion found in some kidney cells.

nepioconch: an early-formed part of the dissoconch of bivalves, separated from the later part by a discontinuity.

neritic: pertaining to the shallow waters from the low tide mark to the 200 m isobath.

neuston: organisms associated with the surface film of water.

nidamental glands: paired organs that secrete outer, gelatinous, protective layer on eggs of many oegopsid cephalopods.

non-planate: see planate.

notalian: see antiboreal.

notum: shield-like dorsum of shell-less opisthobranchs or those with internal shells, and pulmonates; may be separated from the ventral hyponotum by a keeled perinotum or a perinotal groove in pulmonates.

nuchal cavity: a shallow mantle cavity in Patellogastropoda and some Cocculiniformia.

nuchal lobes: see neck flaps.

nucleus: in gastropods, the first whorl of the protoconch (not recommended) or the protoconch itself (outdated usage); centre of any spiral or set of concentric rings, such as the earliest-formed part of the operculum.

nurse cells: = paraspermatozoa.

nurse eggs: undeveloped eggs in an egg capsule that are consumed by developing larvae.

nymph: narrow, crescentic attachment area for ligament on postero-dorsal margin of valve.

obconical: bluntly conical.

oblique sculpture: in bivalves, that which is neither commarginal nor radial; may also be divaricate.

odontophore: comprising the odontophore 'cartilage', protractor and retractor radular muscles of gastropods, and the radula that covers most of its surface.

oesophageal glands: pocket-like outgrowths of the mid-oesophagus; lined with a glandular epithelium that secretes digestive enzymes.

oesophageal pouches: small pouches at or near the junction of the oesophagus and buccal cavity in caenogastropods.

oesophageal valve: flap-like valve between the oesophageal opening and the radular sac; prevents regurgitation of food when the odontophore protrudes.

oesophagus: usually divisible in gastropods into the anterior oesophagus, the mid-oesophagus, which includes the length affected by torsion, and the posterior oesophagus, which opens to the right wall of the stomach.

oligolecithal: eggs with little yolk.

oligomerisation: evolutionary process of narrowing of the radula and reduction in numbers of teeth.

oligopyrene spermatozoa: see paraspermatozoa.

oligotrophic: low in nutrients.

ontogenetic descent: increase with age and growth in the depth inhabited by an organism.

oodiaulic: diaulic reproductive system in which the vas deferens and vagina share a common duct, and the oviduct is separate; compare androdiaulic.

ootheca: simple, lens-shaped egg capsule attached directly to a hard substratum.

opaline gland: repugnatory gland within the mantle cavity of aplysiomorph anaspideans.

operculigerous: presence of an operculum.

operculum: a horny or calciferous plate; partially or completely closes the aperture on retraction into the shell; present in prosobranch gastropods, larval stages in some marine pulmonate families and adult *Salinator* and *Amphibola*; see also epiphragm.

opisthocline: inclined backwards with respect to the direction of growth of **helicocone** shell; see also **prosocline**.

opisthodetic: see **ligament**.

opisthogyrate: **umbo** curved to point posteriorly.

oral disc: a terminal expansion of the snout of 'prosobranchs', often modified, for example, by a midventral division, papillae or tentacular fringe.

oral lappets: feelers or tactile flaps on each side of the mouth.

oral shield: cuticular, innervated structure ventral to the mouth of chaetoderm aplacophorans; may assist in food detection and burrowing.

oral tentacles: pair of tactile organs present around the mouth of some opisthobranchs.

oral veil: membrane above the mouth in some opisthobranchs.

orbicular: subspherical, orb-like.

orthochoanitic: descriptive of short, cylindrical **septal neck** in nautiloids.

orthocone: a straight nautiloid shell.

orthocline: perpendicular to the direction of growth of the **helicocone** in gastropods, or to hinge axis in bivalves.

orthogyrate: **umbo** points inwards, towards **umbo** of the opposite valve.

orthurethran: condition in which ureter is long and straight; secondary specialisation of the kidney that opens near the pneumostome; excretory products are released within the pulmonary cavity; compare **mesurethran**, **sigmurethran**.

osphradium: chemosensory organ near the **ctenidium**.

ostiole: end of capillary surrounded by muscle fibres that can occlude the opening and regulate blood flow into the haemocoel in pulmonates.

ostracum: calcified layers of the **shell**.

Otoceran zone: the lowest Triassic zone, marking the Permian–Triassic Boundary; characterised by shells of the ammonites *Otoceras woodwardi* and, more commonly, *Ophiceras* species.

outer fold: see **mantle folds**.

outer lip: the outer edge of the **aperture** from the **suture** to the **columella**; forms the generating curve of the gastropod shell.

oviducal glands: secrete inner, gelatinous, protective layer on eggs of teuthoid cephalopods; forms tip of egg stalk and cement to fix eggs of octopodid forms to substratum.

oviduct: general term for egg-conducting tube; extends from the ovary to the mantle cavity in gastropods and comprises several glandular regions.

oviparity: deposition of eggs in which development and hatching are completely external; compare **ovoviviparity** and **viviparity**.

ovipositor: places eggs during laying and may form the spawn mass.

ovotestis: single gonad comprising discrete ovary and testis in opisthobranchs.

ovoviviparity: development and brooding of eggs within parent's body, hatching internally, or soon after laying; compare **oviparity** and **viviparity**.

pachydont: hinge dentition comprising large, massive and usually rounded teeth.

paedogenesis: see **paedomorphosis**.

paedomorphosis: form of **heterochrony** in which sexually mature animals show somatic features typical of the early developmental stages seen in related taxa; reflects either retarded somatic development (**neoteny**) or accelerated reproductive development (**paedogenesis**).

pallets: paired calcareous periostracal structures that close the burrow when the siphons are retracted; in teredinid bivalves.

pallial: relating to the **mantle**.

pallial cavity: = **mantle cavity**.

pallial curtain: = **inner fold**.

pallial edge: see **mantle edge**.

pallial gonoduct: portion of reproductive tract derived from **ectoderm**; comprises most glandular and copulatory structures.

pallial grooves: shallow reduced remnant of **mantle cavity** in polyplacophorans; also termed **branchial cavity**.

pallial line: thin incised line indicating attachment of bivalve **pallial** (= **mantle**) **retractor muscles**.

pallial oviduct: portion of oviduct in the mantle cavity of gastropods; derived from **ectoderm**.

pallial retractor muscles: arise along the **pallial line** and insert into mantle edge in bivalves; undertake mantle expansion and retraction.

pallial sinus: posterior indentation of **pallial line** in bivalves where siphonal retractor muscles attach.

pallial skirt: see **mantle skirt**.

pallium: = **mantle**.

palp proboscis (proboscides): process(es) on each **labial palp**; used for feeding on surface detritus in protobranch bivalves.

papillary sac: vetigastropod left kidney, in which numerous papillae project into the lumen.

paralarval stage: cephalopod of first post-hatching growth stage that is **pelagic** in near-surface waters during the day, and has a distinctly different mode of life from that of older conspecific individuals (after Young & Harman 1988).

paraphyly, paraphyletic: pertaining to a group including the ancestor but not all of its descendants; see **polyphyly** and **monophyly**.

parapodia: thin, lateral, wing-like expansions of the foot in some opisthobranchs; used to protect the shell or for swimming.

paraspermatozoa: non-fertilising spermatozoa, also termed **nurse cells**; either anucleate (**apyrene**) or that have more (**hyperpyrene**) or less (**oligopyrene**) chromosomes than the haploid number; one of two types of spermatozoa in 'prosobranchs'; see also **euspermatozoa**.

paratroch: the more ventral of two rows of cilia on the **trochophore** of a gastropod, encircling the anus.

parietal wall; pertaining to the broader upper portion of the **inner lip**.

parivincular ligament: longitudinally-elongate, cylindrical ligament located posterior to **beak** in some bivalves.

- parthenogenesis:** reproduction by development of unfertilised eggs to adulthood.
- patelliform:** in the form of a patella or knee cap; like *Patella*, a limpet.
- paucicostate:** sparsely ribbed.
- paucispiral:** with few whorls.
- pavilion:** dorsal extension of the posterior mantle edge of scaphopods.
- pectinibranch:** = **bipectinate** condition: refers to **ctenidia** bearing two rows of gill leaflets.
- pectinate:** comb-like.
- pedal gape:** opening between the valves of a bivalve through which the foot may protrude.
- pedal gland:** general term for any gland associated with the foot; mostly with reference to the mucous gland, usually opening into the transverse groove at the anterior edge of the foot below the **propodium** (occasionally on the side of the **metapodium**), and produces most of mucus over which gastropods creep.
- pedal retractor muscle:** retracts the foot in bivalves, leaves a small scar near the anterior adductor muscle scar.
- pedal sinus:** ventral portion of **haemocoel** in Aplacophora.
- pediveliger:** veliger larva at settlement stage, when the velum is lost and the foot becomes modified for feeding and locomotion.
- pegma:** a solid transverse strut that joins the valves in the umbonal part of the shell, closing it permanently in the fossil group Rostroconchia.
- pelagic:** pertaining to the water column above the sea or lake bed and offshore of the littoral zone; see also **bathypelagic**, **epipelagic**, **mesopelagic**.
- pellicle:** non-calcified larval shell of veliger larva.
- pen:** = gladius.
- penial:** pertaining to the penis.
- penis:** muscular, vascular, erectile tube involved in internal fertilisation in gastropods; may be behind the right cephalic tentacle, a modified **cephalic tentacle**, or arise from the **mantle skirt**; may receive sperm via a **seminal groove** or a closed duct; muscular extension of spermatophoric sac through which bundles of spermatophores pass during copulation in cephalopods; sometimes termed **verge**; see also **terminal organ**.
- pentaganglionate condition:** comprises the arrangement of paired **cerebral**, **pedal**, **pleural** and **parietal ganglia** and the unpaired **visceral ganglion** in many euthyneuran gastropods.
- perforate:** umbilicus present on shell.
- pericalymma:** larva of protobranch bivalves and aplacophorans bearing cilia used for locomotion; derived from term for the outer test. (Greek: *peri* = around, *kalymma* = veil).
- pericardial gland:** site of ultrafiltration of fluid from the blood-auricular walls of vetigastropods, caenogastropods, ventricle and auricle in patellogastropods; each branchial heart of coleoid cephalopods; equivalent of branchial heart in nautiloids.
- pericardium:** sac-like structure enclosing the heart.
- periostracum:** quinone-tanned **conchiolin** forming protective outermost layer of mineralised shell; varies from thin and transparent to thick and fibrous or hairy.
- perispantium:** blood sinus between **siphuncular** filling and the connecting ring in nautiloids.
- peristome:** the lip of the aperture of gastropods and nautiloids.
- phagocytosis:** the process of engulfing foreign material by amoeboid cells.
- phanerobranch:** pertaining to gills that are visible because they cannot be withdrawn into the body, such as in anadoridoidean opisthobranchs; converse of **cryptobranch**.
- pheromones:** secreted substances that influence the behaviour of other individuals.
- phoresy:** transport of a commensal organism by its host.
- photophores:** simple to complex, internal or surficial organs producing bioluminescent light in cephalopods, especially teuthoids.
- photosensitive vesicles:** extra-ocular photoreceptors in coleoids; see also **epistellar bodies**.
- phragmocone:** chambered part of cephalopod shell.
- pilaster:** supporting pillar of tissue.
- pinnate:** arrangement of a series of processes along a central axis, like a feather or comb.
- pinocytosis:** the process of uptake of particles, large molecules and fluid droplets by cells.
- pipe:** secondary, tubular growth of shell emergent from apical (posterior) orifice of scaphopod shell; produced by posterior mantle margin.
- plaits:** folds, usually with reference to the **columella**.
- planate:** strongly compressed, flat-spired shell form of some pulmonates; **non-planate** shells are high-spired.
- planispiral:** coiled in a flat spiral with symmetrical sides.
- plankton:** small, aquatic or aerial organisms that drift with, or are far less mobile than, the currents or winds of their immediate environment.
- planktotrophic:** form of larval development in which benthic eggs hatch as small, free-swimming, shelled veligers; these feed planktonically on algae for up to 30 days before settlement and metamorphosis; see also **lecithotrophic**, **direct development** and **teleplanic larvae**.
- planorbiform:** flat, discoidal shell form resembling that of *Planorbis*.
- plesiomorphy:** retained primitive character state shared with one or more sister taxa; compare **apomorphy**.
- pleural area:** triangular area on the **tegmentum** of intermediate, and some posterior **valves** of polyplacophorans, on each side of the **jugum** and anterior to the lateral area.
- pleurembolic proboscis:** a proboscis in which the distal half may be retracted by muscles inserted distally into the sheath-like, inverted basal half; compare **acrembolic proboscis**.
- pleuroproct:** anus opening to exterior on the right side below the ceratal rows; used previously in superfamilial division of Aeolidina; see also **acleioproct** and **cleioproct**.

pleurothetic: orientated on one side or the other on the substratum, often cemented or attached by a byssus or cemented.

pleuston: buoyant aquatic organisms that live permanently at the water/air surface.

plicae: folds, twists or corrugations.

pneumopore: = **pneumostome** of pulmonates.

pneumostome: a respiratory pore formed by fusion of the mantle border with the neck of pulmonates, usually on right mantle margin; can be closed by a muscle sphincter.

podocyst: structure in pulmonate embryo that regresses before hatching; possibly circulatory in function.

podocytes: specialised excretory cells involved in ultrafiltration of the blood in post-metamorphic molluscs; situated in the cardiac region between the haemocoel and pericardial coelomic spaces; see **pericardial gland**.

polydont: form of radula with many teeth in each transverse row; = **polystichous**.

polygyrous: = **multispiral**.

polyphyly, polyphyletic: group comprising two or more taxa derived from distinct lineages; see **monophyly** and **paraphyly**.

polyspermy: fertilisation involving the entrance of several sperm into the egg, only one of which forms a pronucleus.

polystichous: form of radula with many teeth in each transverse row; = **polydont**.

polytrochous larva: second larval stage of Gymnosomata, characterised by three ciliary bands for locomotion.

porcelanous: shell surface lustrous and smooth like porcelain.

postbranchial space: see **prebranchial chamber**.

posterior area: part of bivalve shell demarcated from rest in some way, usually by an umbonal ventral ridge and/or by a difference in sculpture; the area of the polyplacophoran **tegumentum** on the posterior part of the posterior valve.

posterior canal: see **siphonal canal**.

posterior pedal gland: opens near the centre of the metapodium.

posterior valve: the posteriormost valve of a polyplacophoran.

prebranchial chamber: dorso-lateral part of mantle cavity in coleoid cephalopods, separated by the gills from the postbranchial space.

precephalic tentacles: sensory appendages on anterior fold of mantle in some carnivorous polyplacophorans.

prismatic layer: outer calcified layer of the shell, comprising columnar prisms of calcite or aragonite in a mesh of conchiolin.

prismatonacreous: primitive shell microstructure; comprises prismatic layer of calcitic or aragonitic prisms between outer **periostracum** and inner **nacreous** (mother-of-pearl) layer.

pro-ostracum: free forward-projecting region of the middle plate of the gladius in Vampyroteuthidae.

proboscis sac: retaining structure for the elongate proboscis present in some groups, such as the Melongenidae; also synonym of **proboscis sheath** of Conoidea.

proboscis sheath: covering of the **proboscis**; comprises the head in Conoidea, in which it is also called the **labial tube**.

proboscis: an elongate, tubular extension of the pretentacular area of the head in neogastropods that is retractile within a **proboscis sheath**; eversible extension of the mouth in pseudothecosomes and gymnosomes.

procerebrum: lobe associated with cerebral ganglia of pulmonates, neurosecretory in function, and main synapomorphy of this group; thought to be homologous with opisthobranch rhinophoral gland.

proctodeum: terminal invagination of the ectoderm; precursor of anus.

prodissoconch: larval shell in bivalves; may comprise the **prodissoconch I**, secreted by larval **shell gland** before planktonic feeding, and the **prodissoconch II**, secreted by the larval mantle edge during planktonic feeding.

promyal chamber: chamber that allows water to pass between the posterior byssal retractor and the adductor muscle.

propodium: anterior part of the gastropod foot.

prosocline: inclined forwards with respect to the direction of growth of the **helicocone** shell; see also **opisthocline**.

prosogyrate: **umbo** curved to point anteriorly, as in most bivalves.

prostate gland: part of the male **pallial gonoduct** producing seminal secretions; may line part of **vas deferens** or form a separate diverticulum opening into the **vas deferens** or the penis in 'prosobranchs' and opisthobranchs.

protandry: maturation of male reproductive organs before female organs in the same individual; see also **consecutive hermaphroditism**.

protobranch: primitive leaf-like ctenidial form characteristic of Protobranchia.

protoconch: larval shell of a gastropod or a shelled cephalopod; in gastropods, the **protoconch I** is formed in the egg capsule or by the **shell gland** of the developing larva before planktonic feeding; the **protoconch II** is formed during planktonic feeding, in neritopsines, caenogastropods and heterobranchs only.

protogyny: maturation of female reproductive organs before male organs in the same individual; see also **consecutive hermaphroditism**.

protonephridia: embryonic excretory organs in polyplacophoran, bivalve and gastropod larvae.

protoplax: a flat, spear-shaped accessory plate covering the antero-dorsal margin of most Pholadidae.

protostyle: mucus-bound, usually rod-shaped food string in some gastropods, scaphopods and protobranch bivalves; see **crystalline style**.

prototroch: row of locomotory cilia below the level of the mouth around the body of the **trochophore** larva.

provinculum: in Pectinoidea a narrow, vertically striated area on each side of the resilifer; central area of the hinge of larval bivalves.

pseudo-operculum: hardened mucous plug secreted in aperture of non-operculate land snails (see also **epiphragm**); oval thickening of connective tissue on dorsal surface of the tail in two charopid genera; analogous in function to the operculum of prosobranchs.

GLOSSARY

- pseudobranch:** gill developed in mantle cavity of some basommatophoran pulmonates; also termed **secondary** or **accessary gill**.
- pseudoconch:** transparent structure of conchiolin in the thecosome family Cymbuliidae; not homologue of a shell.
- pseudocopulation:** transfer of spermatozoa or **spermatozeugmata** from juxtaposed male to female in the water currents entering the mantle cavity of the female.
- pseudectenodont:** **ctenodont** hinge dentition derived secondarily from forms with longitudinally elongate teeth.
- pseudofaeces:** particulate waste matter inhaled by suspension feeders and coated with mucus before ejection from the mantle cavity.
- pseudohermaphroditism:** presence of non-functional reproductive organs of one sex in an individual functionally of the other sex, usually a small penis in female.
- pseudolamellibranch:** symmetrical, W-shaped form of ctenidia, with connected filaments, in palaeoheterodonts and some pteriomorph bivalves.
- pseudolateral tooth:** lateral tooth with its proximal end close to the **beak**.
- pseudopallium:** sac-like structure, derived from the snout, that covers the base of the shell in some Eulimidae.
- pseudoproboscis:** an extension of one side of the snout rolled to form an incomplete tube, as in Capulidae, Turbinidae and some Trochidae.
- pseudosigmurethrous condition:** folds of the mantle roof forming a structurally open, functionally closed, sigmurethrous ureter.
- pseudosiphon:** the enrolled edge of the mantle within the shell slit of pleurotomariids and dome fissurellids, that directs the exhalant flow of water from the mantle cavity.
- ptenoglossate radula:** with numerous, similar, fang-like teeth; sometimes spelled 'ctenoglossate'.
- pteropod:** a long-established, but no longer accepted name for the unrelated Thecosomata and Gymnosomata.
- pulmonary cavity:** highly vascularised, dorsal wall of the pulmonate mantle cavity used for breathing air.
- pulmonary sac:** = **pulmonary cavity**.
- puncta, punctae:** fine pore(s) or pit(s).
- punctate:** covered with fine pores or pits.
- pupiform:** cylindrical, with rounded ends, resembling an insect pupa, and the gastropod snail genus *Pupa*.
- pycnonéphridien:** caenogastropod renal type in which the primary and secondary lamellae of the renal organ are separated; compare **méronephridien**.
- pyriform:** pear-shaped.
- Quenstedt muscle:** one of a pair of small muscles, attached to a shell valve; probably homologous with anterior pedal muscles.
- quincunx, quincuncial:** arranged in group of five.
- r-selection:** appropriate to variable or transient conditions; populations fluctuate greatly; promotes **semelparity** and brood protection; see **K-selection**.
- rachiglossate radula:** each row composed of a central tooth flanked each side by a lateral tooth.
- radial:** sculpture radiating from the umbo towards the ventral margin of bivalves.
- radial aperture:** one that is coplanar with the coiling axis of a gastropod, *i.e.* perpendicular to the direction of coiling.
- radula:** a ribbon of chitin bearing teeth in regular longitudinal and transverse rows in the buccal cavity.
- radular caecum:** a dorsal cavity between the radular sheath and buccal cavity in some 'prosobranchs'.
- radular cartilages:** paired skeletal structures, cartilage-like in nature, that together with muscles comprise the **odontophore** and underlie and support the **radula**.
- radular formula:** the form and number of **central**, **lateral** and **marginal teeth** in each radular row.
- radular membrane:** supportive structure for radular teeth.
- radular sac,** a blind diverticulum of the buccal cavity, in which the radular teeth are formed, and which extends posteriorly from the **odontophore**.
- radular teeth:** classified as **central**, **lateral** and **marginal**; **lateral** and **marginal** distinguish between different forms of teeth on each side of the single, bilaterally symmetrical **central** or **rachidian tooth**, also termed **median tooth**; similar **lateral** and **marginal teeth** may jointly be termed **latero-marginal**; **uncinal teeth** occur between the **lateral teeth** and **marginal plates** of polyplacophoran radulae; teeth adjacent to, and almost indistinguishable from, the **central tooth** may be termed **central teeth** in pulmonates.
- ramose:** branched.
- raphes:** apposed paired ciliated ridges on the floor and roof of the opisthobranch mantle cavity, that create an exhalant water current through the cavity.
- rastriform:** rake-like.
- 'Receptaculites':** order of globular Palaeozoic (Ordovician–Permian) fossils of uncertain systematic affinity.
- rectus:** straight.
- reinforcement sac:** = **crystal sac**.
- renal gonoduct:** a short, ciliated duct linking gonadal and pallial ducts in caenogastropods, derived from the right kidney.
- renal organ:** = **kidney**.
- renopericardial canal:** conducts primary urine from the pericardial cavity to the kidney.
- repugnatory glands:** produce chemical repellents for defensive purposes; see also **opaline gland**.
- resilifer:** hollowed out depression on the **hinge plate** marking attachment of internal layer of **ligament** in bivalves; a spoon-shaped, projecting form is termed a **chondrophore**.
- resilium:** internal ligament of bivalves.
- reticulate:** sculpture formed by intersection of spiral and **prosocline** or **opisthocline** elements, *i.e.* not crossing at right angles as in **clathrate** sculpture.
- retrograde:** backward motion or direction, with reference to locomotory waves in gastropod foot.
- rachidian tooth:** see **radular teeth**.

rachidian tooth: see **radular teeth**.

rhinophore: well-developed, paired, chemosensory tentacle on the head of nudibranchs, usually capable of retraction; homology with those of sacoglossans or anaspideans uncertain; sensory organ below eye of cephalopods, possibly chemosensory.

rhpidoglossate radula: central, lateral and marginal teeth developed, usually with four or more lateral teeth and many marginal teeth in each row.

rhynchodeum: a permanent probosceal sheath in the Conoidea.

rhyncholites: fossilised mandibles or beaks of unknown cephalopods, some of which probably belong in order Nautilida.

rhynchostome: the aperture through which the proboscis is protruded.

rhynchoteuthion: larva of ommastrephid cephalopods, with distinctive tentacles, fused up to 1–10 mm mantle length.

rhythmic consecutive hermaphroditism: regular changes of sex occur in each individual.

rimate: cavity with a narrow lumen.

salinity: the total mass of salts in water, usually seawater, expressed in parts per thousand (‰).

scaphoconch: a secondary larval shell present in the echinospira larva.

schizodont: variation on **heterodont** dentition in some Trigonioidea, comprising a few strong teeth radiating from below the umbones, and a broad, bifid central tooth on the left valve.

sculpture: surface structure and ornamentation on shell surface.

secondary gills: developed in mantle cavity of marine and freshwater pulmonates; also termed a **pseudobranch** or **accessory gill**; lamellate or bipinnate structure in mantle cavity of some opisthobranchs generally not thought to homologous with the **ctenidium** of other gastropods; **cerata** of Aeolidina, **circum-anal gills** in Doridina and the dorso-lateral **dendritic 'gills'** in Dendronotina are not homologous with **ctenidium**.

selenizone: narrow spiral band on the shell formed of crescentic growth lines reflecting the semicircular end of a notch or slit in the outer lip, as in pleurotomarioideans.

semelparity: death after a single reproductive season.

seminal groove: ciliated genital groove in gastropods along which sperm are transported to the penis during copulation; equivalent to the closed **vas deferens** in more highly derived forms.

seminal receptacle: sac for reception and possible long-term storage of **exogenous sperm**; frequently at the proximal end of the **oviduct** or **gonoduct**; see also **bursa copulatrix**.

seminal vesicle: diverticulum or swelling of visceral part of **vas deferens** for temporary storage of **endogenous sperm**; see also **ampulla**.

sepiion: internal, calcareous **shell** of sepioid cephalopods; also termed 'cuttlebone'.

septal foramen: opening in **septum** of nautiloids for passage of **endosiphuncle**.

septal neck: adapical (posterior) extension of **septum** around **septal foramen** of nautiloid cephalopods.

septation: the process of division of shell or visceral regions by one or more **septa**.

septibranch: **ctenidial** form of some carnivorous Anomalodesmata, modified as a muscular perforated septum used to trap prey.

septum, septa: structural partition(s) or division(s) between two shell or visceral regions, or within a **haemocoel**; partitions dividing **phragmocone** of nautiloid **shell**.

setiform: bristle-like.

shell gland: ectodermal area that secretes the larval shell; applied to the dorsal and ventral glands that open together on the mantle edge and contribute to post-larval shell formation.

shell muscle: attachment of the body to the shell; usually paired but ranging from eight in Monoplacophora to one in higher vetigastropods and caenogastropods; homologous with **columellar muscle** of gastropods;.

sigma-T: expression of seawater density at temperature T (°C) and salinity S (‰ or parts per thousand by weight), where $\text{sigma-T} = (\text{density value} - 1) \times 10^3$.

sigmurethran: condition in which ureter follows the intestine anteriorly to the mantle edge; water-resorbing structure opening externally via pneumostome; compare **mesurethran**, **orthurethran**.

simultaneous hermaphroditism: ovary and testis, or ovotestis produces gametes simultaneously in one individual.

sinusigera: S-shaped edge to outer lip of protoconch II.

sipho: fleshy cord of tissue extending posteriorly from body through the **septal foramina** in nautiloid cephalopods.

siphon: elongation of mantle edge to form a tubular passage for inhalant or exhalant water flow in bivalves and gastropods; raised tube on posterior edge of cephalic shield in Gastropteridae.

siphonal canal: tubular or trough-like extension of aperture supporting and enclosing the **inhalant siphon** (anterior canal) and the **exhalant siphon** (posterior canal).

siphonal fasciole: group of strongly curved growth lines near base of columella marking previous positions of **siphonal notch**.

siphonal notch: narrow indentation in the margin of the aperture near the base of the columella in caenogastropods, through which the inhalant siphon protrudes.

siphonal process: formed of fused **inhalant siphon** and **exhalant siphon**.

siphonal retractor muscles: modified **pallial retractor muscles** that withdraw posteriorly directed siphons in siphonate bivalves; attachment point marked by **pallial sinus**.

siphonoplax: a tubular, secondary, calcareous or conchiolin structure protecting the siphons of most Pholadidae.

siphuncle: a long, slender tube extending from the **protoconch** through all chambers (or **camerae**) of a nautiloid cephalopod and perforating the **septa**; comprises the **ectosiphuncle** and **endosiphuncle**.

slit: in gastropods a shallow to deep, narrow slot on the **outer lip**, as in Pleurotomariidae; in polyplacophorans, a narrow slot on the **insertion plate**, subdividing it into teeth.

socket: a groove or hollow on the hinge of a bivalve, accommodating a tooth on the opposite valve.

soleniform: elongated shell, as in the bivalve genus *Solen*.

- sorting area:** ciliated, ridged part of stomach wall and caecum.
- spadix:** formed of four modified buccal tentacles in *Nautilus*; used to pass a sperm rope to the female.
- spatfall:** the settling and attachment of veliger larvae, often *en masse*.
- species-group:** includes all taxa at the ranks of species and subspecies.
- sperm bulbs:** transferred and exploded spermatophores of ommastrephid squids; comprise a sperm mass and the adhesive contents of cement body that glue the sperm bulb to the seminal receptacle.
- sperm duct:** duct carrying sperm; several non-homologous structures within Mollusca.
- sperm sac:** a general term for an exogenous sperm storage structure.
- spermatheca:** = bursa copulatrix.
- spermathecal sacs:** receptacles for spermatophores on the buccal membrane or in the mantle in some cephalopods.
- spermatic bulb:** a distinct sac at the end of the penis in the opisthobranch taxa *Hamineobulla*, Smaragdinellidae and Runcinoidea.
- spermatocyst:** = seminal receptacle.
- spermatophore:** a thin-walled sac containing massed sperm that may be placed in the partner's body by copulation, pseudocopulation or injection.
- spermatophore sac:** receives the spermatophore during copulation.
- spermatozeugmata:** a combination of active euspermatozoa attached to oligopyrene or apyrene paraspermatozoa; in some Ptenoglossa only.
- spermoviduct:** see hermaphroditic duct.
- spiral:** parallel to the direction of growth of the helicocone in gastropods.
- spiral caecum:** arises from the posterior globular part of the stomach in vetigastropods; reduced or lost in caenogastropods.
- spiral cleavage:** cleavage pattern of early embryonic cells of molluscs, such that the positions of the upper one of two divided cells lies slightly offset from the lower one, forming a spiral pattern.
- spout:** a rudimentary siphonal canal in a gastropod shell.
- statoconia:** small calcareous accretions in the statocyst of many molluscs.
- statocyst:** paired, innervated, spherical organ of balance; lined with cilia, and may hold a single statolith, numerous statoconia or both.
- statolith:** large calcareous concretion in the statocyst.
- stenocalymma:** scaphopod larval form, intermediate between pericalymma larva of Neomeniomorpha and trochophore of conchiferans.
- stenohaline:** tolerant only of a narrow range of salinities; converse euryhaline.
- stenothermic:** tolerant only of a narrow range of temperatures, converse eurythermic.
- stereoglossate:** radula type associated with a flat odontophoral bending plane, allowing no lateral splaying of the radula at its most functional point; compare flexoglossate.
- stimulator:** structure associated with penis, probably used in mate stimulation.
- stomodeum:** anterior region of the embryonic alimentary tract; formed by ectodermal invagination.
- streptoneury:** torsion of the visceral loop of gastropods to form an asymmetric figure-of-eight, such that the connective from the right pleural ganglion crosses to the left over the oesophagus on its way to the visceral ganglia, and that from the left pleural ganglion passes to the right side beneath the oesophagus.
- striate:** marked with fine grooves.
- strobilation:** asexual reproduction by transverse fission of the body; known in Thecosomata.
- style:** a general term for a crystalline style or a protostyle.
- style sac:** anterior part of the stomach that compacts faecal matter; contains crystalline style or protostyle.
- subequivalve:** valves almost equal in size.
- subpallial cavity:** the groove surrounding the shell muscle between the foot and the mantle in caudofoveate and some other limpets.
- subradular organ:** presumed chemosensory structure in subradular pouch or anterior buccal cavity of polyplacophorans, monoplacophorans, nautiloids and several basal gastropod groups; also termed licker.
- subradular pouch:** blind sac on posterior wall of buccal cavity of polyplacophorans, containing subradular organs.
- subrenal sinus:** near columellar muscle at the base of the visceral mass; distributes blood through the respiratory organs and the kidney *en route* to the heart.
- subtrigonal:** close to triangular.
- suprabranchial chamber:** portion of mantle cavity dorsal to the ctenidia in bivalves.
- sutural laminae:** anterior, wing-like extensions of the articulamentum on valves II to VIII of polyplacophorans, projecting forwards beneath the posterior margin of the preceding valve.
- sutural plates:** = sutural laminae.
- sutural ramp:** an outward-sloping, flattened, convex or concave area on many gastropods, below (abapical to) the suture and delimited by the shoulder angle.
- suture:** continuous line on gastropod shell surface along the junction of the whorls.
- symbiont:** participant in a symbiotic relationship between two organisms, commonly different species; broadly includes all interactions, such as parasitism; more narrowly, restricted to mutually beneficial interactions.
- symplesiomorphy:** a primitive character state shared by two or more taxa.
- synapomorphy:** derived character shared by two or more sister taxa.
- synaptorhabdic:** lamellae of ctenidia linked by interlamellar septa, forming a reticulate pattern; in bivalves.
- systole:** contraction phase in the beat of the heart.

taenioglossate radula: row of seven teeth, comprising two marginals and one lateral on each side of a **central** or **rachidian tooth**; in most caenogastropods and some lower Heterobranchia.

tail valve: posterior shell plate of polyplacophorans.

talon: = fertilisation pouch–seminal receptacle complex in pulmonates; sometimes simple and finger-like, or complex (bipartite or tripartite).

tangential aperture: lies oblique to the coiling axis of a gastropod and tangential to the surface of the **last whorl**.

taxodont: hinge dentition with numerous, straight or chevron-shaped teeth arranged regularly along the **hinge plate** in some bivalves.

tegumentum: shell layer between **periostracum** and **articulamentum** of Polyplacophora; composed of conchiolin and calcium carbonate.

teleoconch: post-larval gastropod shell.

teleplanic larvae: planktotrophic larvae with a protracted planktonic life, and potentially capable of widespread dispersal (Greek: *tele* = far, *planos* = wandering).

telolecithal: eggs well supplied with yolk, concentrated at the vegetal pole.

tentacles: applied to any long appendage, such as **cephalic tentacles**, mantle edge tentacles, and muscular appendages on the head of cephalopods.

terminal organ: penial organ of coleoid cephalopods.

terminal pipe: a short tube protruding from the apex of some scaphopods.

testicular duct: = **vas deferens**.

tetrataxic: wave form, in which locomotory waves traverse the foot as four separate systems of waves; see also **monotaxic** and **ditaxic**.

thread: a very fine, elongate, raised sculptural element.

torsion: the rotation by 180° of the visceral mass on the head-foot in an anticlockwise direction during gastropod development; all structures passing between head, foot and visceral mass are affected.

torted state: see **torsion**.

Tournaisian: lowermost stage of Lower Carboniferous in European stratigraphic system.

toxoglossate radula: comprises single pairs of long, slender, hollow, barbed marginal teeth; in Conoidea.

trabecula(e): band(s) of muscular or fibrous supportive tissue within an organ or tissue layer.

transverse: perpendicular to the long axis of a scaphopod; an obsolete term for 'axial' in gastropods, but describes sculpture on cowries that is not longitudinal.

trapeziform: rectangular in form, with two parallel sides.

trema, tremata: small oval or circular opening(s) in shell (for example, haliotids) analogous to the pleurotomariid and scissurellid **slit**, through which water flows, and sensory pallial tentacles project.

Tremadocian: European stage in Lower Ordovician; above Dolgellian of Cambrian, below Arenigian.

triaulic: reproductive morphology in which the ectodermally derived **vas deferens**, **vagina** and **oviduct** are physically as well as functionally separate; these components transport **endogenous sperm**, **exogenous sperm**, and fertilised eggs, respectively; see also **monaulic** and **diaulic**.

trochophore: the first larval stage in molluscs; biconical in form, with two ciliary bands, the **prototroch** and **paratroch**; a shell is lacking; resembles annelid and platyhelminth larvae, phyla that also exhibit **spiral cleavage**; see also **polytrochous larva**.

truncate: shortened abruptly.

turbiniform: broadly conical spire and convex base; resembling the shell of *Turbo*.

typhlosoles: longitudinal folds on the ventral stomach wall that move and direct particles of food and waste towards the intestine.

umbilicus, umbilicate: presence of, or pertaining to, an indentation of varying depth at the axial base of a spiral shell.

umbo: dorsal region of maximum curvature of **valve**, extending to, and possibly coinciding with, the **beak** of a bivalve.

uncinal teeth: see **radular teeth**; also referred to as **uncini**.

ureotelic: nitrogenous waste excreted primarily as urea.

uterus: female glandular portion of oviduct between **carrefour** and **vagina** in basommatophoran pulmonates; secretes outer layers of egg mass.

vagina: receives **exogenous sperm** for the fertilisation of endogenous eggs; sometimes termed **vestibule** in caenogastropods.

valve: element of a shell composed of more than one part, such as the left or right valve in bivalves or one of the eight plates in polyplacophorans.

valve of Leiblein: prevents regurgitation from the oesophageal region when the proboscis is extended; at junction of anterior and mid-oesophagus; in neogastropods.

varix, varices: thickened elevation(s) on the shell, indicative of growth reduction during which a thickened lip developed.

vas deferens: transfers **endogenous sperm** from the testis to the penis in **androdiaulic** and **triaulic** forms; male pallial gonoduct also comprises the **prostate gland**.

vegetal pole: at one end of longitudinal axis of cleavage in the fertilised egg; linked with formation of digestive and associated organs.

veliconcha: larval form that becomes benthic directly after hatching.

veliger: uniquely molluscan larva, characterised by the **velum** (Latin: = sail), that develops from the **protoconch** and comprises two large ciliated lobes used for feeding and swimming.

velum: see **veliger**.

venter: undersurface of shell in Nautiloidea, distinguished by presence of a hyponomic sinus.

ventral sinus: see **pedal sinus**.

verge: = **penis**.

vermiform: worm-like.

GLOSSARY

vestibule: entrance or antechamber to another chamber or space; papillate, innervated organ antero-dorsal to mouth of neomenioid Aplacophora; protrusible hydrostatically; may detect food; used also for **vagina**.

visceral loop: comprises the visceral and oesophageal ganglia and their connectives.

visceral sinus: returns blood from the visceral mass of gastropods to the heart.

visceral sole: posterior part of the sole of the foot in some opisthobranchs.

visceropallium: posterior part of cephalopod, comprising mantle, mantle cavity and organs, and shell and fins when present; upper part of gastropod body, comprising the visceral mass and mantle.

vitellogenesis: process of yolk accumulation around the egg.

vitreous: glassy, transparent.

viviparity: production of live offspring within the body of the adult; compare **ovoviviparity** and **oviparity**.

volution: see **whorl**.

Whiterockian: lowermost stage in the Middle Ordovician of the North American stratigraphic system.

whorl: one complete spiral turn of a univalve shell.

wing: lateral expansions of the foot, or **parapodia**, in opisthobranchs; lateral expansions of the central teeth in some prosobranch gastropods.

yellow gland: a gland in the mantle cavity of Aglagidae that produces a yellow fluid when the animal is disturbed; of uncertain function, it may produce alarm pheromones.

zooxanthellae: symbiotic dinoflagellates in many cnidarians; obtained by predation and retained alive in the tissues of some nudibranchs and in tridacnid clams.

zygoneury: development of neural connections, termed **zygoses**, in caenogastropods between the supra-intestinal and left pleural ganglia, and between the subintestinal and right pleural ganglia.

zygoses: see **zygoneury**.

LITERATURE

- Arnold, W.H. (1965). A glossary of a thousand-and-one terms used in conchology. *Veliger* 7, Supplement
- Bates, R.L. & Jackson, J.A. (eds) (1987). *Glossary of Geology*. American Geological Institute : Alexandria 3rd edn x 788 pp.
- Beu, A.G. & Maxwell, P.A. (1990). Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey Palaeontological Bulletin* 58: 52–61.
- Bloom, W. & Fawcett, D.W. (1975). *A Textbook of Histology*. W.B. Saunders : Philadelphia 10th edn xv 1033 pp.
- Brusca, R.C. & Brusca, G.J. (1990). *Invertebrates*. Sinauer Associates Inc. : Massachusetts 922 pp.
- Cox, L.R. (1960b). General characteristics of Gastropoda. Pp. 184–1169 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press : Boulder, Colorado & Lawrence, Kansas
- Cox, L.R. (1969). General features of Bivalvia. Pp N3–N129 in Moore, R.C. (ed.) *Treatise of Invertebrate Paleontology. Part N. Mollusca 6. Vol. 1. Bivalvia*. Geological Society of America & University of Kansas Press : Boulder, Colorado & Lawrence, Kansas
- Humphrey, C.L. & Simpson, R.D. (1985). The biology and ecology of *Velesunio angazi* (Bivalvia: Hyriidae) in the Magela Creek, Northern Territory. Report to the Office of the Supervising Scientist, October 1985 476 pp., 127 tabs, 122 figs
- Lincoln, R.J. & Boxshall, G.A. (1987). *The Cambridge Illustrated Dictionary of Natural History*. Cambridge University Press : Melbourne 413 pp.
- Lincoln, R.J., Boxshall, G.A. and Clark, P.F. (1982). *A Dictionary of Ecology, Evolution and Systematics*. Cambridge University Press : Cambridge viii 298 pp.
- Parker, S.P. (ed.) (1989). *McGraw-Hill Dictionary of Scientific and Technical Terms*. McGraw-Hill : New York 4th edn 2088 pp., appendices.
- Ride, W.D.L., Sabrosky, C.W., Bernardi, G. & Melville, R.V. (1985). *International Code of Zoological Nomenclature*. University of California Press : Berkeley xx 338 pp.
- Shepherd, S.A. & Thomas, I.M. (1989). Pp. 497–900 in *Marine Invertebrates of South Australia part II*. Handbook of the Flora and Fauna of South Australia. South Australian Government Printer : Adelaide
- Tiechert, C. (1964). Glossary of morphological terms used for nautiloids. Pp K54–K59 in Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology Part K Mollusca 3 Cephalopoda – General Features – Endoceratoidea – Actinoceratoidea – Nautiloidea – Bactritoidea*. Geological Society of America & University of Kansas Press : Boulder, Colorado & Lawrence, Kansas
- The New Encyclopedia Britannica* (1984). Encyclopaedia Britannica : Chicago 15th edn 30 vols.
- Wiley, E.O. (1981). *Phylogenetics: the Theory and Practice of Phylogenetic Systematics*. John Wiley & Sons: New York xv 439 pp.
- Young, R.E. & Harman, R.F. (1988). 'Larva', 'paralarva' and 'subadult' in cephalopod terminology. *Malacologia* 29: 201–207

INDEX

To minimise duplication of entries, the index has been arranged either by taxa with a subordinate subject or concept (for example, nearly all generic and/or specific names) or *vice versa*, as for those taxa above family level. With a few exceptions, information relating to families may be found most readily *via* the *family treatment* entry for each family. All taxa above genus have been listed for a number of selected subjects, to assist comparisons and collation of information across the volume. They include all references to: *diversity* of taxa in a general sense, *endemism* and *diversity in Australia*; the *fossil record, in toto*, by era and by period; *fisheries, introduced taxa* and *pest species*; some behavioural traits such as *burrowing* and *boring*; reproductive characteristics including *spawning* and *spermatophores*, *oviparity*, *ovoviviparity*, *viviparity* and *parental care*; *shell* and *shell ultrastructure*, and; Australian islands and territories, such as *Lord Howe Island, Norfolk Island* and *Antarctica*. Fg = Figure; Pl = Plate; Tb = Table; all other numbers refer to pagination.



- abalone, 667
 - annual catches, Tb 1.3
 - economic importance, 73
 - fisheries, 73
 - food and exploitation, 669
 - harvesting, 73
 - status of fisheries, 73
- Abderospira*, 956
- Aboriginal resources, 339, 347
 - Anadara* spp., 256
 - Bivalvia, 195
 - Cellana* spp., 644
 - Fragum unedo*, 330
 - Heterodonta, 305
 - Hyriidae, 293
 - molluscs in diet, 72
 - Neritidae, 700
 - Patellogastropoda, 644, 645
 - Pyrazus ebeninus*, 722
 - Solenioidea, 341
 - Teredinidae, 371, 374
 - turban shells, 676
- Abra*, 344
- Abralia andamanica*, 521
 - external appearance, Fg 13.11
 - spawning, 521
- Abralia astrolineata*
 - breeding season, 521
- Abralia trigonura*
 - alimentary tract, Fg 11.14
- Abraliopsis*
 - photophores, Fg 11.6
- Abraliopsis gilchristi*, 521
 - breeding season, 521
 - external appearance, Fg 13.11
- abundance
 - Cardiidae, 330
- Abyssochitonidae, 161
- Abyssochrysidae, 708
- Acanthaster planci*, Fg 1.31
 - and *Charonia tritonis*, 35, 801
- Acanthina spirata*
 - spines and predation, 622
- Acanthoceras*, Cretaceous, 99
- Acanthochites* (*Notoplax*), 177
- Acanthochitona*, 188
 - Acanthochitona approximans*, 188
 - Acanthochitona bednalli*, Fg 3.41, 188
 - Acanthochitona communis*, 188
 - Acanthochitona crinita*, 188
 - Acanthochitona defilippii*, 188
 - Acanthochitona hirundiniformis*, 175, 188
 - Acanthochitonidae, Fg 3.41, Pl 9
 - colouration, 164
 - family treatment, 188
 - Acanthochitonina*, 188
 - Acanthochitoninae, 161, 188
 - Acanthodoris*, 992
 - Acanthopecten*, Permian, 97
 - Acanthopleura*, 170, 187, 188
 - extrapigmentary ocellus, Fg 3.20
 - as human food, 175
 - Acanthopleura arenosa*, 187
 - Acanthopleura curtisiana*, 187
 - Acanthopleura echinata*, 165, 167, 169
 - anatomy, Fg 3.9
 - Acanthopleura gaimardi*, 187
 - spawning, 173
 - Acanthopleura gemmata*, Fg 3.39, 161, 185, 187
 - homing, 175
 - shell valves, Fg 3.1
 - spawning, 186
 - Acanthopleura granulata*, 185, 186
 - Acanthopleura hirtosa*, 166, 187
 - spawning, 24, 186
 - Acanthopleura japonica*, 185, 186
 - Acanthopleura miles*, 187
 - Acanthopleura spiniger*, 186
 - Acanthopleura spinosa*, Pl 8, 187
 - as human food, 175
 - Acanthopleurinae, 185
 - Acar celleporacea*
 - Tertiary, Fg 1.101
 - Acaroceras*, 493
 - Acavoidea, description, 1093
 - acceptance grooves, Fg 5.3
 - Nuculidae, 237
 - accessory boring organ, 622
 - Caenogastropoda, Fg 15.13
 - Muricidae, 822
 - Muricoidea, 820
 - Naticidae, Fg 15.13, 790
 - Naticoidae, 790
 - accessory fin, Fg 13.26
 - Grimalditeuthidae, 538
 - accessory plates, Pholadidae, 375
 - accessory salivary glands
 - Costellariidae, 844
 - Neogastropoda, 819
 - prosobranchs, 620
 - Acephala, 5
 - Acesta*, distribution, 268
 - Acetabularia*, 967
 - acetabuliferous arms
 - Gymnosomata, 986
 - Pneumodermatidae, Fg 16.66, 986
 - Acetes sibogae australis*, 519
 - acetylcholine
 - Bivalvia, 210
 - Pulmonata, 1048
 - Acharax*, 241
 - Acharax agassizi*
 - as sablefish prey, 244
 - Acharax eremita*, distribution, 243
 - Achatina fulica*, 69, 70, 109, 1061, 1089, 1090
 - diet, 1055
 - dispersal, 1089
 - distribution, 1055
 - eggs and hatchlings, Fg 17.49
 - embryogenesis, 1051
 - external appearance, Fg 17.21
 - jaw, Fg 17.49
 - memory retention, 577
 - as pest species, 1055
 - radula, Fg 17.49
 - reproductive tract, Fg 17.49
 - shell, Fg 17.49
 - vector of *Angiostrongylus cantonensis*, 69, 1090
 - Achatinella*, captive breeding, 112
 - Achatinellidae, Fg 17.40
 - affinities, 86
 - family treatment, 1080
 - Achatinelloidea, description, 1080
 - Achatinidae, Fg 17.21, Fg 17.49, Tb 1.5
 - family treatment, 1089
 - Achatinoidea
 - description, 1087
 - families, 1087
 - Achatinoinei, 1086
 - Acholoe vittata*, 175
 - acid secretion, Cassidae, 794
 - Acila castrensis*
 - feeding, 237
 - valve dentition, Fg 5.2
 - acinous glands, Madrellidae, 1009
 - Acleioprocta, 1011
 - Aclididae, Fg 15.153
 - Australian fauna, Tb 15.1, 813
 - diversity in Australia, 817
 - family treatment, 816
 - Aclis*, 816, 817
 - Aclis microscopica*
 - shell, Fg 15.153
 - Aclis minor*, 817
 - Aclophora hedleyi*
 - radula, Fg 15.149
 - Aclophoropsis univitta*
 - operculum, Fg 15.148
 - Acmaea*, 648
 - protandrous hermaphroditism, 23
 - Acmaea digitalis*
 - homing behaviour, 577
 - Acmaea mitra*, 648, 649
 - Acmaea parva* var *tasmanica*, 640
 - Acmaea scabra*
 - homing behaviour, 577
 - Acmaeidae, Fg 15.34, Fg 15.37, Tb 15.1, 639, 641, 646
 - characters, 648
 - family treatment, 648
 - taxonomic history, 648
 - Acmaeinae, 641
 - characters, 649
 - Acmaeioidea, 639, 641, 646
 - Australian diversity, 648
 - description, 648
 - habitat, 648
 - link to Nacelloidea, 645
 - taxonomic revision, 639
 - Acochlidea
 - characters, 959
 - relationships, 940
 - spermatophores, 936
 - Acochliidae, Fg 16.40
 - external appearance, Fg 16.40
 - family treatment, 960
 - Acochlioidae, characters, 960
 - Acochlidium*, 960
 - Acochlidium fijiense*, Fg 16.40
 - external appearance, Fg 16.40
 - Aconchoidea, 962

INDEX

- Aconeceras*, Cretaceous, 99
acrembolic proboscis, Fg 15.12
formation, 619
Acroloxidae, Fg 17.17
Acroloxus lacustris
reproduction, Fg 17.17
Acropsis, 257
acrosome, prosobranchs, 634
acrosome ultrastructure
Hyriidae, Fg 7.5
Palaeoheterodonta, Fg 7.5
Trigoniidae, Fg 7.5
Acrosterigma, 331
Acrosterigma cygnorum
distribution, 331
external appearance, Fg 8.16
Acrosterigma dupuchense, 331
Acrosterigma elongata
affinities, 331
Acrosterigma magna, 331
Acrosterigma marielae
distribution, 331
Acrosterigma reeveanum
distribution, 330
as fossils, 331
in middens, Fg 1.36
shell, Fg 8.15
Acrosterigma rugosa
distribution, 330
Acrosterigma vlamingi
distribution, 331
Actenidiacea, 941
Acteocina, 948–950
egg masses, 949
Acteocina atrata, 949
Acteocina canaliculata, 949
Acteon, Fg 16.3, Fg 16.16, 586,
930, 932, 934, 936, 943, 944
internal anatomy, Fg 16.3
nervous system, Fg 16.16
organisation, Fg 16.1
Acteon pelecis, 944
Acteon tornatilis, 937, 944
Acteonidae, Fg 16.4, Fg 16.11,
Fg 16.12, Fg 16.16,
Fg 16.21, 943
epidermal glands, Fg 16.7
family treatment, 943
gut morphology, Fg 16.12, 927
jaw plate, Fg 16.11
relationships, 940
Acteonoidea, 943
characters, 943
Actinaria
as epitoniid prey, 816
Actinia tenebrosa, 1012
Actinoceras, 490
Silurian, 95
Actinoceratoidea, 485
Actinocerida, 487, 490
Actinocyclus, 997
Actinoleuca, 639
Actinoleuca multiradialis
Oligocene, 645
Actinopterella, Silurian, Tb 1.6
Actinopteria, Tb 1.6
Devonian, Tb 1.6, 95
Silurian, Tb 1.6
activity cycles
Bivalvia, 219
Unionoidea, 219
Acutospira, 718
Adalaria, 54, 992
Adalaria proxima
chemoreception, 577
Adamnestia arachis, 919, 948, 949
external appearance, Fg 16.27
shell, Fg 16.27
Adams, Arthur, 7, 162, 196, 1038
Adams, Henry, 162, 196
Adamsoceras, 490
Adamussium colbecki, 277
Adavale Basin, Fg 1.95
Adclarkia dawsonensis
external appearance, Fg 17.70
Addisonia, 658
Addisonia lateralis, 662
external appearance, Fg 15.46
Addisonia paradoxa, shell,
Fg 15.45
Addisoniidae, Fg 15.45, Fg 15.48,
Fg 15.50, 658
affinities, 663
shell asymmetry, 653
adductor muscle scars, 267, 314
Arcticoidea, 348
Bivalvia, Fg 4.4, 199
Crassatelloidea, 325
Lucinoidea, 310
Mactroidea, 336
Pholadomyoidea, 406
terminology, Fg 4.10, Fg 4.11
Tridacnoidea, 332
Trigonoidea, 295
adductor muscles, 277, 347, 414
Anomalodesmata, 399
Anomioidea, 280
Arcoidea, 253
Bivalvia, Fg 4.1, Fg 4.5, 13, 195,
204
Cardioidea, 328
Carditoidea, 322
Corbiculoidea, 352
Corbulidae, Fg 8.42
Crassatelloidea, 302
Cyamioidea, 302
Galeommatoidea, 302
glochidium, 292
Heterodonta, 302
lamellibranch, Fg 4.5
Lucinoidea, Fg 8.5
Myoidea, 363
Ostreinae, 270
Ostreoida, 268
Palaeoheterodonta, 289
Pandoroidea, 415
Pectinoidea, 275
Pholadoidea, 372
Protobranchia, Fg 4.5
Pteriomorpha, 249
reduction, 205
Solenioidea, 340
terminology, 199
Teuthoidea, 455
Thracioidea, 407
Tridacnoidea, 302
Veneroidea, 355
Adelacerithiinae, 810
Adelaidean region, 78, 593
Adenopoda, 2
Adeorbidae, 772
adhesion in prosobranchs, 612
adhesive organ
Idiosepiidae, 514
Adipicola
habitat, 253
Admetinae, 845
diversity in Australia, 846
Admetula
distribution, 846
Adrenella, 240
Adulomya
as fossils, 241
Adusta, 780
Aegires, 995, 996
distribution, 996
Aegires albopunctata, 996
Aegires albus, 996
Aegires citrina, Fg 16.79, 996
radula, Fg 16.79
Aegires punctilucens, 996
Aegires sublaevis, 996
Aegires villosus, Fg 16.79
external appearance, Fg 16.79
Aegiretidae, Fg 1.28, Fg 16.79, 990
family treatment, 995
Aegopinella nitidula
impact on native molluscs, 58
Aelurostrongylus abstrusus, 68
Aenigmabonus, 658
Aeolidia papillosa, 1012
Aeolidiella foulisi, Fg 16.103, 1012
external appearance, Fg 16.103
radula, Fg 16.103
Aeolidiidae, Fg 16.11, Fg 16.19,
Fg 16.103, 936
camouflage, 939
diet, 938
family treatment, 1012
jaw plate, Fg 16.11
nematocyst storage, 938
Aeolidina, 990
cerata, 923
characters, 1011
external features, Fg 16.2, 923
internal anatomy, Fg 16.3
Nudibranchia, 990
Aeolidiopsis harrietae, Fg 16.11,
1012
jaw plate, Fg 16.11
Aeolidiopsis ransonii, 1012
Aequipten, swimming, 277
aerial respiration, Mytilidae, 219
aerobic metabolism
intertidal bivalves, 212
Aesopus, distribution, 829
Aesopus pallidulus
shell, 827
Aesopus plurisulcatus
shell, Fg 15.160
aesthetes, Fgs 3.17–3.19, 161, 171
aestivation, 1106
Austropeplea tomentosa, 64
Camaenidae, 1113
Helicidae, Fg 17.71, 1113
Helicodiscidae, 1100
Pulmonata, 1055
Pupillidae, 1082
Sphaeriidae, 218, 305
Subulinidae, 1087
terrestrial molluscs, 56, 625
affinities
Cardiidae, 331, 336
Cystopeltidae, 1107
Heterodonta, 305, 306
Neritopsina, 694
non-marine molluscs, 80, 85
Palaeoheterodonta, 293
Plesiotrochidae, 737
Rhytididae, 1093
Seguenzioida, 692
Tridacnidae, 336
Afossochiton, 188
Africotrion, 846
Afrocardium, 331
Afropisidium, 82
Agathiceras, Permian, 97
age at maturity
Achatinidae, 1089
Aplacophora, 148
Arcidae, 256
Bivalvia, 29
Camaenidae, 1113
Donacidae, 347
Enidae, 1086
Helicidae, 1113
Hyriidae, 298
Idiosepiidae, 514
Limacidae, 1102
Loliginidae, 519
Loligo opalescens, 519
Nautilus, 494
Ommastrephidae, 532
Pinnidae, 267
Prochaetodermatidae, 148
Psammobiidae, 345
Pteriidae, 262
Tridacnidae, 335
Veneridae, 356
Vesicomysidae, 351
age determination
Idiosepiidae, 514
Loliginidae, 519
ageing, Coleoidea, 470
aggregation, Crassostreinae, 272
Aglaja, Fg 16.8, Fg 16.18, 937,
952, 974
haemocoel, Fg 16.8
reproduction, Fg 16.18
Aglaja inermis, Fg 16.17
Hancock's organ, Fg 16.17
Aglajidae, Fg 16.4, Fg 16.6,
Fg 16.8, Fg 16.12,
Fgs 16.16–16.18, Fg 16.31,
Pl 33, 926, 932, 939
body cavity, Fg 16.8
copulation, 934
diet, 937
evolution, body/shell, Fg 16.4
family treatment, 952
gut morphology, Fg 16.12
Hancock's organ, Fg 16.17
predation, 583
as retusid predators, 950
sensory bristles, Fg 5.15
Agriolimax
intestinal passage rate, 1044
locomotion, Fg 17.6
Agriolimax agrestis
oxygen consumption, 1046
Agriolimax reticulatum
uricotel, 1046
Agriolimax sp.
eye structure, Fg 17.15
Agriopoma, habitat, 360
Aillyidae, 1102
Aioloceras, Cretaceous, 99
Akebiconcha, 348
Akera, Fg 16.16, 929, 947, 975
nervous system, Fg 16.16
Akera bayeri, 975
Akera bicincta, 975
Akera bullata, 975
swimming, 925
Akera soluta, Fg 1.44, Fg 16.56,
42, 975
external appearance, Fg 16.56
shell, Fg 16.56
swimming, 925
Akeridae, Fg 1.44, Fg 16.16,
Fg 16.56
family treatment, 975
Akerioidea, 974, 975
Akibumia, 798
osphradium, 799
shell, 798
Akibumia flexibilis, 798
Akibumia orientalis, 798
protoconch, Fg 15.139
shell, Fg 15.139
Akibumia schepmani, 798
Alaba, 708, 714, 715
Alaba incerta, 715
external appearance, Fg 15.87
operculum, Fg 15.87
radula, Fg 15.87
Alaba opiniola, shell, Fg 15.87
Alaginella, 841

- Alathyria*
distribution, 82, 298
glochidium, 59
in fluvifaunulae, 81
- Alathyria condola*, 298
hinge dentition, Fig 7.2
- Alathyria jacksoni*, 297, 298
habitat, 59, 60
limiting factors, 60
Mitchellian fluvifaunula, 81
pearls, 297
resistance to desiccation, 60
shell form, Fig 1.67, 60, 199
- Alathyria pertexta*, 298
- Alathyria profuga*, 61, 298
- Albatross*, 145
- Albian*, 820
- Albimanus*, 410
- albumen*
Volutidae, 835
- albumen gland*, 587
Caenogastropoda, 616
Haminoea zelandiae, Fig 16.18
prosobranchs, 632
- Alcithoe*
as fossils, 835
prostate gland, 632
testicular duct, 632
- Alcyna*, shell, 683
- Alcyonacea*, as glaucid prey, 1013
- Alcyonaria*
as epimeniid prey, 156
as nudibranch prey, 938
- Alcyonidium*, as corambid prey, 991
- Alcyonium*, 785
- Alderia*, 973, 974
- Alderia modesta*, 974
ceratal pumping, 929
- Alderopsis*, 973, 974
- Aldisidae*, 997
- Aldrovandi*, 431
- Alectryonella*, shell, 272
- Alectryonella plicatula*
embedding, 272
- Alepisaurus*, 526, 531, 533
- Alepisaurus ferox*, 510, 511, 538,
546, 547, 551, 552, 554
- Alepisaurux borealis*, 552
- Aletes squamigerus*, Fig 15.129
- algae*
and intertidal molluscs, 30
- Aliculastrum*, 954, 955
- Aliculastrum cylindricum*, 955
- alimentary tract, 349, 419, 745,
806, 1063
ancestral gastropod, 585
Anomalodesmata, 399
Anomiidae, 281
Anomioidea, 280
Architectonicoidea, 858
Basommatophora, Fig 17.7
Bathysciadiidae, 656
Bivalvia, Fig 4.13, 195, 208
Cancellarioidea, 845
Carditoidea, 322
Cephalopoda, 459
Cerithioidea, Fig 15.90, Fig 15.94
Cingulopsioidea, Fig 15.103
Coleoidea, Fig 11.14, 500
Conoidea, 847
Ellobioidea, Fig 17.37
evolutionary trends, 616
Gastropoda, Fig 14.21, 585
Heterobranchia, Fig 15.186
Heterodonta, 302
Lepetelloidea, Fig 15.49
Mollusca, 14
Muricoidea, Fig 15.155, 820
Myoidea, 364
Mytiloidea, Fig 6.1
- Naticoidea, 790
- Neogastropoda, Fig 15.155,
Fig 15.164, Figs
15.168–15.171, 822
- Octopoda, Fig 11.14
- Omalogyroidea, 864
- Opisthobranchia, Fig 14.26,
Fig 16.12
- Palaeoheterodonta, 290
- Patellogastropoda, 641
- Pholadomyoidea, 406
- Polyplacophora, Fig 3.8
- prosobranchs, 616
- Ptenoglossa, Fig 15.150
- Pulmonata, Fig 14.27, Fig 17.2,
Fig 17.7, Fig 17.39, 1042
- Pyramidelloidea, Fig 15.186, 865
- Scaphopoda, 434
- Sepioidea, Fig 11.14, 459
- Solemyoidea, 241
- Stylommatophora, Fig 17.7,
Fig 17.39, 586
- Teuthoidea, Fig 11.14, 459
- Thracioidea, 407
- Tonnoidea, Fig 15.143
- Triphoroidea, Fig 15.150, 808
- Valvatoidea, 856
- Vampyromorpha, Fig 11.14
- Veneroidea, 356
- Aliomactra*, 339
- Aliptinae*, 811
- Allan, Joyce, 11, 499, 569, 920
- Allogastropoda, 606, 854
plesiomorphies, 854
status, 567
- Alloteuthis*, shell, 517
- Alloteuthis africana*
sexual dimorphism, 517
- Alloteuthis subulata*
sexual dimorphism, 517
- Allotrioceratidae, 488
- Alococoncha*, Tb 1.6
- Aloidiidae*, 366
- Aloidis gibba*, 366
- Alternaria*
transmission by molluscs, 72
- Alvania*, 751
distribution, 751
tentacles, 745
- Alvania novanensis*
protoconch, Fig 15.108
shell, Fig 15.108
- Alycyna*, shell, Fig 15.63
- Amadeus Basin*, Fig 1.95
- Amaea*, Cretaceous, 99
- Amalda*
diversity in Australia, 837
- Amalda hilgendorfi*
in deep-water, 835
- Amaltheidae*, 770
- Amathia biseriata*, 840
- Amathina*, 771, 775, 868, 869
buccal region, Fig 15.187
- Amathina tricarinata*, 868, 869
shell, Fig 15.187
ventral surface, Fig 15.187
- Amathinidae*, Fig 15.187, Tb 15.1,
944
as bivalve parasites, 868
family treatment, 868
hosts, 869
- Amaurochiton*, 187
- Amblemididae*, 296
- Amblychilepas*, 669
- Amblychilepas nigrita*, Pl 22
shell, Fig 15.54, 671
- Ambonychia*
Ordovician, 92
Silurian, Tb 1.6
- Ambonychiidae*, 250
- Ameloctopus litoralis*, Pl 19
eggs, 549
- Amerianna*,
biogeography, 1056
copulatory organ, 1072
distribution, 84
origin, 1074
shell, 64, 1072
- Amerianna carinata*
copulatory organ, Fig 17.33
radula, Fig 17.33
shell, Fig 17.33
- Americardia*
shell/body relationship, Fig 4.10
- Amesodesma*, 340
- Amiantis*
habitat, 360
nymph, 356
- Amiantis callosa*
shell and hinge, Fig 8.37
- Amicula*, 184
- Amimopina*, 1085
Gondwanan origin, 1086
radula, 1085
- Amimopina beddomei*, 1085
- Amimopina macleayi*, 1085
affinities, 86
distribution, 1085
pallial configuration, Fig 17.45
pseudosigmoethy, 1085
reproduction, Fig 17.45, 1085
shell, Fig 17.45, 1085
ureter, Fig 17.12
- amino acids
octopine, 340
strombine, 340
- ammonia excretion
Agriolimax reticulatum, 1046
terrestrial molluscs, 56
- Ammonia laevis*, 504
- ammoniacal cephalopods, 457,
500, 527, 538, 542
- Ammonocera*, 864
- Ammonocera sucina*
external appearance, Fig 15.185
shell, Fig 15.185
- Ammonitellidae*, distribution, 1112
- ammonium ions, 463
cephalopod buoyancy, 463, 501
Cranchiidae, 463
Nautilidae, 463
- Ammonoidea*
Carboniferous, Fig 1.99
Cretaceous, Fig 1.100, 99
Devonian, Fig 1.98
Jurassic, 97
Permian, Fig 1.99, 97
- ammonotely, 16, 17
Bivalvia, 210
Cephalopoda, 463
Coleoidea, 501
Heterodonta, 303
Polyplacophora, 169
- amoebocytes, 929
- Aplacophora, 147
- Bivalvia, 210
- Cephalopoda, 462
- Polyplacophora, 167
- Scaphopoda, 434
- Tridacnidae, 209, 302
- Amonellipsites*, Carboniferous, 97
- Amoria*, 833
distribution, 835
as fossils, 835
- Amoria exoptanda*, Pl 28
- Amoria lineata*, radula, Fig 15.164
- Amoria undulata*, shell, Fig 15.164
- Amoria zebra*
as prey, Fig 14.23
shell collection, 76
- Amphibola*, 1067
hypobranchial gland, 1067
veliger, 27
visceral commissure, 1067
- Amphibola crenata*
egg mass, 25
juvenile, Fig 1.21
- Amphibolidae*, Fig 1.20, Fig 1.21,
Fig 1.48, Fig 17.19, Fig 17.29
family treatment, 1067
juvenile, Fig 1.21
operculum, 1039
- Amphibolis*, 39
- Amphibolis antarctica*, 175, 958
- Amphiboloidea*
description, 1067
- Amphidesmatidae*, 339
- Amphidromus cognatus*, 1112
distribution, 85
- Amphimeniidae*, Fig 2.2
- Amphineura*, 2
- Amphiperas*, 784
- Amphiperatidae*, 784
- Amphiplica*, 662
- Amphiplica gordensis*, habitat, 661
- Amphiplica knudseni*
alimentary tract, Fig 15.49
- Amphipoda*, as ovulid prey, 836
- Amphithalamus*, 747
- Amphithalamus incidatus*
protoconch, Fig 15.106
shell, Fig 15.106
- Amphitretidae*, Fig 1.54, Fig 13.33
family treatment, 546
- Amphitretus pelagicus*, 546
adult, Fig 1.54
external appearance, Fig 13.33
larva, Fig 1.54
radula, Fig 13.33
- Amplirhagada*
age at maturity, 1051
feeding, 1054
growth rate, 1051
reproductive cycle, 1051
shell, 1112
- Amplirhagada castra*
in Scrub Fowl diet, 1112
- Amplirhagada elevata*
shell, Fig 17.69
- Ampullariidae*, 71, 628, 706
buccal pouches, 621
gas exchange, 580, 625
subradular organ, 630
- Ampullarioidea*, Tb 15.1, 567, 610
affinities, 703
description, 706
in Palaeozoic, 606
- Ampullina*, Cretaceous, 99
- Ampullospirinae*, 790
- Amsterdam Island*
Argobuccinum pustulosum, 801
Ranella australasia, 801
- Amusium*, 219, 277, 278, 774
bucephalid trematodes, 277
defensive behaviour, 220
pallial eyes, 213
swimming, 206, 219, 277
- Amusium balloti*, 277
catches, Fig 1.79
fishery, 74, 220, 277
shell, Fig 6.18
State fisheries, Fig 1.80
- Amusium pleuronectes*, 277
catches, Fig 1.79
diet, 277
distribution, 74

INDEX

- fecundity, 277
fishery, 74, 220, 277
foot, 277
musculature, 205
shell, Fg 6.18
State fisheries, Fg 1.80
- Amygdalum*, 253
gills, 251
kidneys, 251
rectum, 251
- amylase, 14, 364, 1043
in Gastropoda, 586
style, 15
- Anabarella*, Cambrian, Fg 1.97, 89
- Anabathridae*, Fg 15.106, Tb 15.1, 745
family treatment, 747
oviduct, 745
prostate gland, 632
- Anabathron*, 747
- Anabathron contabulatum*
head-foot, Fg 15.106
shell, Fg 15.106
- Anabathron luteofuscus*
operculum, Fg 15.106
radula, Fg 15.106
shell, Fg 15.106
- Anachis*
gastric shield, 829
penis, 829
prey, 829
shell, 827
- Anadara*, 254, 256
burrowing, 254
diversity in Australia, 256
habitat, 256
haemoglobin, 256
heart, 256
hinge, 254
Quaternary, 101
as ranellid prey, 800
sculpture, 254
shell, 254
- Anadara antiquata*, 256
in middens, Fg 1.36
- Anadara crebricostata*, 256
shell, Fg 6.2
- Anadara granosa*, 256
Aboriginal resources, 256
development, 256
- Anadara trapezia*, 254
Aboriginal resources, 256
distribution, 256
endemic, 256
fishery, 76, 221, 256
habitat, 256
internal morphology, Fg 6.2, 254
mantle cavity, Fg 6.2
in middens, 72
spawning season, 256
- Anadarinae*, 254
- Anadoridoidea*, characters, 990
diet, 938
external features, Fg 16.2
families, 990
Nudibranchia, 990
rhizophore, Fg 16.17
- anaerobiosis
amino acids, Solenoidea, 340
Bivalvia, 211
- Anaflemingites*, Triassic, 97
- Anagaudryceras*, Cretaceous, 99
- Anaitides williamsi*
trochophore larvae, Fg 1.1
- anal gland
function, 819
Muricoidea, 819
Neogastropoda, 819
Pseudolivinae, 836
Turbinellidae, 825
- Anapella*, 339, 340
endemism, 340
habitat, 340
- Anapella cycladea*
as fossils, 340
shell, Fg 8.23
- Anapella variabilis*, as fossils, 340
- Anaspidea*, 917
characters, 974
diet, 937
external features, Fg 16.2, 922
- Anaspyroceras*, Silurian, 95
- Anatimya*, 412
- Anatinellidae*, 337
- Anatoma*, 666
- Anatoma australis*, shell, Fg 15.52
- Anchura*, Cretaceous, 99
- Ancillinae*, distribution, 835
- Ancillista*
diversity in Australia, 837
- Ancillista cingulata*
external appearance, Fg 15.165
swimming, 836
- Ancillista muscae*, Pl 29
- Ancillista velesiana*
shell, Fg 15.165
- Ancistrocheirinae*
characters, 521
as sperm whale prey, 521
- Ancistrocheirus*, 521
eggs, 521
gladius, 453
as shark prey, 521
- Ancistrocheirus lesueuri*
radula, Fg 13.12
- Ancistrolepisinae*, 827
- Ancistroteuthis*, fin, 524
- Ancylastrum*
affinities, 84
biogeography, 1056
copulatory organ, 1072
distribution, 84, 1074
shell, 65, 1039, 1072
shell sculpture, 1072
- Ancylastrum irvinae*, Fg 17.33
copulatory organ, Fg 17.33
jaw, Fg 17.33
radula, Fg 17.33
shell, Fg 17.33
- Ancylidae*, Fg 17.17, Fg 17.32, Tb 1.4
affinities, 1056, 1072
family treatment, 1071
form groups, 63
in freshwater, 62, 63
secondary gills, 18
- Ancylus fluviatilis*
reproduction, Fg 17.17
- Ancyropoda*, component groups, 3
- Andara crebricostata*
hinge plate, Fg 4.6
- Aneitea*, distribution, 1109
- Aneitiella*
distribution, 1109
radula, 1109
- anemones, as epitoniid prey, 813
- Angaria*, 674, 675
- Angaria delphinus*, 674
head-foot, Fg 15.56
radula, Fg 15.56
shell, Fg 15.56
- Angaria gibbuloides*, as fossils, 675
- Angaria imparigranosa*
as fossils, 675
- Angaria incisa*, 674
- Angaria tetragonostoma*
as fossils, 675
- Angaria tyria*, 674
- Angariidae*, 673, 674
- Angariinae*
in Australia, 673
description, 674
- Angas, George Fife, 9
- Angas, George French, Fg 1.8, 9, 196, 236, 568, 569, 920, 1038
illustrations, Fg 1.9
- Angasiella*, 994
- Angasiella edwardsi*, Fg 1.9
- Angiola*, 722, 724
bioluminescence, 722
- Angiostrongylus cantonensis*, 68, 70
Achatina as vector, 1090
distribution, 69
in humans, 69
life cycle, 69
snail vectors, 1056
- Angiostrongylus vasorum*, 68
- Angolypta launcestonensis*
Fg 17.1, Fg 17.52
- Angrobia*, 83
- Angyomphalus*, Carboniferous, 95
- Anidolyta*, 977
- anisakiasis, Ommastrephidae, 533
- Anisoceras*, Cretaceous, 99
- Anisocorbula*, shell, 366
- Anisodonta*, 321, 322
distribution, 322
- Anisodonta alata*, 321
- Anisodonta angulata*, 321
- Anisodonta caledonica*, 322
- Anisodonta subalata*, 322
shell, Fg 8.11
- Anisus*, as fossil, 1058
- Annelida
relationship to molluscs, 1
spiral cleavage, 22
- Annulipulsellum*, 444
- Anodonta*, 291
filtration rate, 291
glochidium, Fg 4.21
osmoregulation, 291
- Anodonta woodiana*, 214
brooding, 214
- Anodontia*, Tertiary, 101
- Anodontophora*, Triassic, 97
- Anodontopsis*, Silurian, Tb 1.6
- Anoglypta*, 1093
- Anoglypta launcestonensis*, 1058, 1093
- Anomalocardia*, 358
nymph, 356
- Anomalocardia squamosa*
intertidal distribution, 43
shore zonation, Fg 1.45
- Anomalodesmata*, 225
aorta, 401
behaviour, 402
biogeography, 404
characters, 226
classification, 405
description, 397
distribution, 404
ecology, 402
euspermatozoa, 20
excretion, 401
external appearance, shell, 397
fossil record and phylogeny, 404
history of discovery, 397
life history, 402
mantle apertures, 204
morphology and physiology, 397
nacre, 202
natural history, 402
nervous system, 401
reproduction, development, 401
sense organs, 401
- Anomalodiscus*, habitat, 358
- Anomia*, 281
byssal notches, 280
Cretaceous, 99
Tertiary, 99
- Anomia descripta*, 281
- Anomia trigonopsis*, 281
- Anomiidae*, Fg 4.12, Fg 6.20
family treatment, 280
- Anomiinae*, 281
- Anomioidea*, 249, 275
description, 280
- Anomphalus*, Devonian, 95
- Antalis*, 436, 439
captacula, Fg 10.6
excretion, Fg 10.9
larval shell, 437
larval stages, Fg 10.12
morphology, internal, Fg 10.3
radula, Fg 10.8
radular bolsters, Fg 10.7
reproduction, Fg 10.9
shell, Fg 10.14
- Antalis antillarum*, 436
- Antalis dentalis*, 436, 439
captacula, Fg 10.6
yolk granules, 436
- Antalis entalis*, 431, 435, 439
captacula, 433
first illustrations, 431
hermaphroditism, 436
spawning, 436
- Antalis inaequicostatum*
burrowing, 433
- Antalis pretiosum*
jewellery, 437
- Antalis vulgaris*, 431, 439
periostracum, 432
- Antarctica
Adacnarc nitens, 260
Adamussium colbecki, 277
Bathyteuthidae, 530
Batoteuthidae, 503
Cirrosteuthidae, 503
Cuspidariidae, 425
Gonatidae, 503
Kondakovia, 524
Laternula elliptica, 412
Lissarca notorcadensis, 260
Neoteuthidae, 503
Philobrya limoides, 260
Philobrya sublaevis, 260
Philobryidae, 260
Phyllomeniidae, 154
Psychroteuthidae, 503
Tomthompsonia, 979
- Anthobranchia*, 941
- Anthothoe albocincta*, 1012
- Anthracopupa*, as fossil, 1081
- Anticorbula*, 350
- antifeedants
Aplysiidae, 977
Chromodorididae, 573, 938, 1000
Granata imbricata, 681
Nudibranchia, 925
Phyllidiidae, 1001
pteroenone, 48
use by amphipod, 48
- Antigona*, 355, 358
habitat, 358
lateral teeth, 358
- Antigona chemnitzii*, 359
- Antiopellidae*, 1009
- Antisabia*, habitat, 771
- Antisabia cranioides*
feeding, 770
- Antisabia erma*, 771
- Antisabia foliacea*, 771
feeding, 770
shell, Fg 15.123

- antiseptic glands
Phenacolepadidae, 700
- Antisolarium*, distribution, 689
- ants as pulmonate predators, 1054
- Anulidentium*, 443
- aortic bulb, 623
- Aperidae, 1091
- apertural barriers, Helicinidae, 702
- apertural canal, Pupinidae, 705
- apertural teeth, Pulmonata, 1039
- aperture
form and function, 614
Gastropoda, 570
Nautiloidea, Fg 12.3
Scaphopoda, 431
Stromboidea, 766
- apex
Dentaliidae, Fg 10.13, Fg 10.14
Entalinidae, Fg 10.19
Fustiariidae, Fg 10.15
Laevidentaliidae, Fg 10.16
Omniglyptidae, Fg 10.18
Scaphopoda, Fg 10.13, 431
- aphally, 708, 744
Cerithioidea, 707
Triphoroidea, 808
- Aphelodoris*, Fg 16.2
external features, Fg 16.2
- Aphrodoctopus*, 544
- Apicalia*, diversity, 817
- Apicalia brazieri*, shell, Fg 15.154
- Apiotrigonia*, Tb 1.6
- Aplacophora, Pl 7
archetype, 2
biogeography, 149
body cavities, 147
characters, 2, 12
circulation, 147
classification, 149
description, 145
embryology, regeneration, 148
excretion, 147
external features, 146
feeding and digestion, 147
gills, 146
history of discovery, 145
methods of study, 149
morphology and physiology, 145
musculature, 13, 146
natural history, 148
nervous system, 147
reproduction, 148
respiration, 147
sense organs, 147
spicules, 146
- Aplysia*, Fg 16.2, Fg 16.3,
Fg 16.15, Fg 16.16, 582,
925, 932, 937, 975–977, 979
chemoreception, 577
circulation, Fg 16.15
copulation, 934
external features, Fg 16.2
heart action, 581
hermaphroditism, 23
internal anatomy, Fg 16.3
learning, 577
mating behaviour, Fg 4.39
nervous system, Fg 16.16
organisation, Fg 16.1
radular function, 583
swimming, 925
- Aplysia brasiliiana*
orientation, 577
swimming, 575
- Aplysia californica*, Fg 16.15, 934
circulation, Fg 16.15
inhibition, 577
- Aplysia cronullae*, 977
- Aplysia dactylomela*, 977
- Aplysia denisoni*, 977
- Aplysia extraordinaria*, 925, 977
- Aplysia fasciata*, Fg 16.9, 925
- Aplysia gigantea*, 925, 975, 977
- Aplysia juliana*, 941, 977
settlement cue, 54
- Aplysia parvula*, Fg 16.57, 941,
976, 977
external appearance, Fg 16.57
organisation, Fg 16.1
- Aplysia punctata*, 976
- Aplysia sydneyensis*, Pl 34, 977
- Aplysiidae, Fg 14.30, Fg 14.31,
Fg 16.9, Fg 16.13, Fg 16.15,
Fg 16.16, Fg 16.57, Pl 34,
975
biology, 937
chemical defence, 573
family treatment, 975
gizzard, Fg 16.13
- Aplysinae
characters, 975
- Aplysinellidae
in diet of *Tylodina corticalis*, 978
- Aplysioidae, 974, 975
characters, 974
- Aplysiomorpha, 940, 974, 977
- Aplysiopsis*, 972, 973
- Aplysiopsis formosa*, 973
- Aplysiopsis orientalis*, 973
- apocrine glands
Iravadiidae, 752
- Apogastropoda
affinities, 694
description, 703
functional kidney, 626
heart, 623
- apomorphies
Neritopsina, 693
Patellogastropoda, Tb 15.2
Vetigastropoda, 664
- apophyses
Martesiinae, 375
Pholadidae, Fg 8.45
Pholadinae, 375
Pholadoidea, 362, 372
Teredinidae, Fg 8.51
- Apoptopegma*, Ordovician, 93
- Aporina delafondi*
intermediate hosts, 68
- Aporodoris*, 941
- Aporrhaidae, 766
- Aporrhais*, 612, 766
- aposematic colouration
Nudibranchia, 990
Opisthobranchia, 918
- Appurdiceras*, Cretaceous, 99
- Aquidauania*, 83
- aragonite, Bivalvia, 202
- Araucaria heterophylla*
on Norfolk Island, 114
- Arborcinea*, 85, 1108
- Arca, 254
eyes, 212
as fossils, 256
habitat, 256
heart, 256
hinge, 254
ligament, 254
nestling, 254
photoreceptors, 212
sculpture, 254
shell, 254
Tertiary, 99
- Arca navicularis*, shell, Fg 6.2
- Arca noae*, eyes, 254
- Archaeogastropoda, 566, 605, 606,
639
status, 567
- Archaeopulmonata, 1047, 1067
- archetypal mollusc, 1
- Archidorididae, 997
- Archidoris*, organisation, Fg 16.1
- Archidoris wellingtonensis*, 941
- Archimediella*, 718
- Archiminolia*, 687
- Architaenioglossa*, Tb 14.1,
Tb 15.1, 610, 620, 703
affinities, 703
characters, 703
status, 567
superfamilies, 703
- Architectonica*, 859, 862
colour, 861
diversity, 861
as fossils, 862
hermaphroditism, 862
locomotion and shape, 575
operculum, 861
radula, 861
- Architectonica grandiosa*
endemic, 861
- Architectonica maxima*, 862
- Architectonica nobilis*, 862
feeding, 862
- Architectonica perspectiva*, 862
head-foot, Fg 15.183
shell, Fg 15.183
spermiogenesis, 862
- Architectonicidae, Fg 15.183,
Pl 29, Tb 15.1, 606, 858
Australian genera, 862
family treatment, 861
protoconch, Fg 1.58, 52
relationships, 606
- Architectonicoidea, Tb 15.1, 566,
854
colonial cnidarians as prey, 858
description, 858
as ectoparasites, 859
phylogenetic significance, 859
- Architeuthidae, Fg 11.2, Fg 11.9,
Fg 11.25, Fg 13.17
family treatment, 527
- Architeuthis*, 527, 528
beak, Fg 11.25
body form, Fg 11.2
eggs, 528
external appearance, Fg 11.9,
Fg 13.17, 527
radula, Fg 13.17, 528
size, 527
- Architeuthis kirki*, 527
- Arcidae, Fg 1.36, Fg 4.6, Fg 4.12,
Fg 6.2, 18
Aboriginal resources, 256
family treatment, 254
on reef flat, 35
- Arcinae, 254
- Arcinella*, 309
shell cementation, 307
- Arcoidea, 249
characters, 225
description, 253
- Arcoidea, 253
description, 253
families, 254
mantle lobes, 204
- Arcopsis*, 257
distribution, 257
as fossils, 258
- Arcopsis adamsi*, 257
- Arcopsis bivia*, 258
- Arcopsis cf. afra*
shell, 257
- Arcopsis pellita*, 258
- Arctica islandica*, 348
heart rate, 211
- Arcticidae, 350
- Arcticoidea
characters, 348
description, 348
- Arctocephalus p. doriferus*
as cephalopod predator, 519, 554
diet, 508
- Arctoceras*, Triassic, 97
- Arcturellina*, 324
- Ardeadoris*, Fg 16.10, 1000
radular teeth, Fg 16.10
- Arene hindsiana*, radula, Fg 15.55
- Arenigian, 93
- Argobuccinum pustulosum*, 801
distribution, 801
shell, Fg 15.142
veliger, 802
- Argonauta*, 453, 552
brooding, 22, 501
chain formation, 51
commensalism, 471
dwarf males, 454
egg case, 501
parental care, 25, 51
sexual dimorphism, 51, 468
shell, 552
sperm transfer, 25, 469
- Argonauta argo*, 552, 554
distribution, 554
function of web, 552
predators, 554
size at maturity, 554
- Argonauta boettgeri*, 552, 554
distribution, 554
eggs, 554
predators, 554
prey, 552
size at maturity, 554
- Argonauta hians*, 552, 554
distribution, 554
egg case, Fg 13.38
egg laying, 554
hectocotylus, Fg 13.38
predators, 554
prey, 554
sexual dimorphism, Fg 13.38
size at maturity, 554
- Argonauta nodosa*, 552, 554
beak, Fg 11.25
distribution, 554
egg case, Fg 13.38
eggs, Pl 21
hatchlings, Pl 21
hectocotylus, Fg 13.38
predators, 554
radula, Fg 13.38, 554
sexual dimorphism, Fg 13.38
- Argonauta oryzata*, 552
- Argonautidae, Fg 11.25, Fg 13.38,
Pl 21
family treatment, 552
- Argopecten*, swimming, 277
- Argyropeza*, 712
function of sculpture, 571
habitat, 709
- Arianta arbustorum*
water loss, Tb 17.1
- arid zone refugia, Fg 1.104
and conservation, 110
- Ariolimax*, stomach, Fg 14.27
- Arion
host of *Davainea proglottina*, 68
shell encapsulation, 1051
- Arion ater*, 1101
behaviour, 1101
distribution, 1100
habitat, 1101
- Arion hortensis*, 1101
distribution, 1100
habitat, 1101

INDEX

- Arion intermedius*, 1101
distribution, 1100, 1101
external appearance, Fg 17.58
feeding, 1101
radula, Fg 17.58
reproductive system, Fg 17.58
withdrawal behaviour, 1101
- Arionidae, Fg 14.27, Fg 17.58,
Tb 1.5
family treatment, 1100
host of *Angiostrongylus cantonensis*, 69
- Arionoidea, description, 1096
- Arionoinci, 1086
- Aristotle, 452, 549
- Arizonella*, Devonian, 95
- arks, 249, 254
Aboriginal resources, 195
- arm crown
Sepiolidae, Fg 13.7
- Armenoceras*, 490
- Armina*, Fg 16.95, 938, 1007, 1008
external appearance, Fg 16.2,
Fg 16.95
- Armina californica*, 1008
- Armina cygnea*, 941, 1008
- Armina punctilucens*, Fg 16.17
rhinophores, Fg 16.17
- Arminidae, Fg 16.17, Fg 16.19,
Fg 16.95, Pl 35, 1007
family treatment, 1007
rhinophore, Fg 16.17
- Arminina, 990
characters, 1007
diet, 938
external features, Fg 16.2, 923
internal anatomy, Fg 16.3
Nudibranchia, 990
- arms, 545, 546
cephalopod musculature, 454
Cephalopoda, 453
Coleoidea, 499
Octopoda, 454
Sepioidea, 454
Teuthoidea, 454, 515
Vampyromorpha, 542
- arrow squid, Pl 18
- Artemia*, 502
- arterial systems
Allotrioceratidae, 488
Cephalopoda, 461
Endocerida, Fg 12.5
Najaceratidae, 488
Nautiloidea, 488
- artesian springs, Fg 1.106
conservation, 111
effects of destruction, 107
endemic fauna, 107
Hydrobiidae, 754
- Arthritica*, 318
density, 41
opportunism, 41
- Arthritica semen*, 219
brooding, 25, 218
development, 218
fecundity, 218
- Arthropoda
spiral cleavage, 22
- Asaphidae, 345
- Asaphis*, 345
dilated midgut, 345
as human food, 346
shell, 345
- Asaphis deflorata*
age at maturity, 345
- Asaphis violascens*
ecophysiology, 345
habitat, 345
in middens, Fg 1.36
- ascaridoid nematodes
Ommastrephidae as hosts, 533
- ascidians
Botryllus schlosseri, Fg 15.24
as columbellid prey, 829
as costellariid prey, 843
as flabellinid prey, 1012
as goniodoridid prey, 992
as marginellid prey, 839
Dendrodoris citrina prey, 1000
as prey of Nembothrinae, 994
as ranellid prey, 800
- Ascobulla*, 932, 937, 938, 940, 947,
961–963
- Ascobulla fischeri*, 963
- Ascobulla ulla*, 963
- Ascocranchia joubini*
nidamental glands, 540
- Ascoglossa, 940
- Ascorhis*, 63, 632, 755
buccal pouches, 753
distribution, 83
external appearance, 755
prostate, 754
sculpture, 752
- Ascorhis tasmanica*
head-foot, Fg 15.111
- asexual reproduction
Cavioliniidae, 980
- Ashby, Edwin, 10, 163, 568
- Aspatharia*
survival without water, 219
- Aspella*
calcified periostracum, 823
shell, 792
- Aspergillidae, 413
- Aspergillum*, 397
- Asperspina brambelli*, Fg 16.42
external appearance, Fg 16.42
- Asperspinidae, Fg 16.42
family treatment, 960
- aspidobranchs, 578
- Aspidopholas*, 375
- Aspidopholas oblecta*
external appearance, Fg 8.48
shell, Fg 8.48
- Assimineae*, 756, 757
diversity in Australia, 757
feeding, 757
as host of *Paragonimus*, 757
- Assimineae buccinoides*, 763
external appearance, Fg 15.113
in mangroves, 45
radula, Fg 15.113
shell, Fg 15.113
- Assimineae tasmanica*, Fg 1.48
- Assimineidae, Fg 1.48, Fg 15.113,
Tb 1.4, Tb 15.1, 606
affinities, 755
in brackish water, 62
family treatment, 756
as hosts of *Paragonimus*, 757
in inland waters, 83
taxonomic status, 107
- Assimineinae, 757
- associations
Calliostoma, sponges, 672
Cypraeidae, sponges, 782
Epitoniidae, 816
Euchelus, sponges, 672
Galeommatidae, 304, 316
Janthinidae, siphonophores,
opisthobranchs, 814
Leiosolenus, coral, 253
Lopha cristagalli, sponges, 272
Lucina floridana, seagrass, 313
Ocythoe, salps, 552
Okadaia elegans, spirorbids, 996
Ovulidae, Cnidaria, 784
- Astarte*
Cretaceous, Tb 1.6
Jurassic, 97
- Astarte africana*, 327
- Astarte longirostris*, 327
- Astarte notailis*, 328
- Astartidae
family treatment, 327
as fossils, 325
- Astartila*, Permian, 97
- Astartila intrepida*
Permian, Fg 1.99
- Astartoidea, 326
- Asteracmea*, 639
distribution, 644
diversity, 651
radula, Fg 15.34
in seagrass, 643, 644, 651
species, 643
Tethyan distribution, 644
- Asteracmea axiaerata*, 651
shell, Fg 15.39
- Asteracmea crebristriata*, 643, 651
- Asteracmea illibrata*, 651
- Asteracmea stowae*, 651
shell, Fg 15.39
- Asteroidea
endemism, 593
as ranellid prey, 800, 801
as scaphopod predators, 437
- Asterolamia*
diversity, 817
- Asteronotidae, 997
- Asteronotus cruenta*, 919
- Asterophilidae, 817
- Asthenothaerus*, 408
- Astocopsis gouldi*
protected species, 112
- Astraea heliotropium*
radula, Fg 15.57
- Astraeinae, 675
- Astraliu*, 675
distribution, 676
- Astraliu tentorium*
shell, Fg 15.57
- Astrolabe*, 196
- Astropecten*
as molluscan predator, 39
- Astrosansonia*, 740
- Astrosansonia dautzenbergi*, 740
protoconch, Fg 15.101
- asymmetry, Gastropoda, 565
- Atactodea, habitat, 340
- Atactodea striata*, shell, Fg 8.23
- Ataxocerithium*, Pl 24
affinities, 811
distribution, 811
protoconch, 811
- Ataxocerithium eximium*, 811
head-foot, Fg 15.150
- Ataxocerithium serotinum*
shell sculpture, Fg 15.150
- Athleta*, 833
distribution, 835
as fossils, 835
head, 833
inhalant siphon, 833
Tertiary, 99
- Athleta studeri*, shell, Fg 15.164
- Athleta subcrenulifera*
Tertiary, Fg 1.101
- Athoracophoridae, Fg 1.61,
Fg 17.4, Fg 17.58, Fg 17.67,
Pl 32, Tb 1.5
colour forms, 1039
family treatment, 1109
Gondwanan origins, 1057
- habitat, 55
retractable tentacles, 1041
- Athoracophorus*
distribution, 1109
- Atlanta*, shell, 804
- Atlanta fossilis*, as fossils, 806
- Atlanta gaudichaudi*, Pl 27
abundance, 804
distribution, 804, 806
external appearance, Fg 15.145
feeding, Fg 1.51
radula, Fg 15.145
- Atlanta peroni*
distribution, 806
shell, 804
- Atlanta turriculata*, Fg 1.53
shell, Fg 15.145
- Atlantidae, Fg 1.14, Fg 1.51,
Fg 1.53, Fg 15.145, Pl 27,
Tb 15.1, 613
in bottom sediments, 980
family treatment, 804
and ocean strider eggs, 49
in plankton, 47
pteropod ooze, 49
as pterotracheid prey, 807
suspension, 804
swarming, 49
- Atomodesma*, Permian, 97
- Atopos*, 1064, 1065
distribution, 1064
diversity, 1064
- Atopos australis*, Pl 31, 1064, 1065
distribution, 1064
external appearance, Fg 17.27
radula, Fg 17.27
reproductive anatomy, Fg 17.27
- Atopos prismatica*
distribution, 1064
- Atreta*, 273, 274
Cretaceous, Tb 1.6
- Atrina*, 265, 266
as fossils, 267
- Atrina pectinata*
shell form, Fg 4.2
- Atrina tasmanica*, 267
shell, Fg 6.12, 265
- Atrina vexillum*, Fg 6.12, 267
shell, 265
- Atrina zelandica* and pea crabs, 267
- attack behaviour, Lolidinidae, 519
- Attenuata*, distribution, 751
- Atthilidae, 1007
- Aturia*, 493
- Aturia stansburienensis*, Fg 12.10
- Aturoidea, 493
- Aturoidea brunnschweileri*,
Fg 12.10
- atypical sperm, 634
- Atys*, 954, 955
- Atys haucum*, Fg 16.33, 954
shell, Fg 16.33
- Atys semistriata*, 955
- Aucellina hughendenensis*, Tb 1.6
Cretaceous, Fg 1.100
- Aculifera, 2
- Aulacopoda, 1060
- Sigmurethra, 1086
- auricle, Bivalvia, Fg 4.15
- auriculo-ventricular valve
Bivalvia, Fg 4.15
- Austerum*, Devonian, 95
- Austraeolis*, 941, 1013
- Austraeolis cacaotica*, Fg 16.104
external appearance, Fg 16.104
- Austral Indo-Pacific Province, 101
- Australaba*, 714
euspermatozoa, 708

- Australian faunas
 prosobranch groups, Tb 15.1
 Opisthobranchia, 941
Australiceras jacki, 99
 Cretaceous, Fg 1.100
Australomya, Permian, 97
Australomya waterhousi
 as fossils, 405
Australoneilo, Tertiary, 99
Australonema, Devonian, 95
Australpera, 355
Austriella sordida, shell, Fg 8.3
Austroassiminea, 757
Austroassiminea lethae
 distribution, 83
 as fossils, 757
Austrobilharzia terrigalensis
 as parasite, 721
 parasite of *Planaxis sulcatus*, 724
 in Silver Gull, 69
Austrochloritis, habitat, 1052
Austrochloritis porteri
 shell sculpture, Fg 17.3
Austrocochlea, 680, 683
 distribution, 683
 habitat, 672
Austrocochlea constricta, Pl 23
 radula, Fg 15.63
 shell, Fg 15.63
 species complex, 683
Austrocochlea porcata, Fg 1.25,
 Pl 3.11, 32
 commensalism, 32
Austrocylichna, 941, 948, 955
Austrocylichna exigua, Fg 16.27
 external appearance, Fg 16.27
 shell, Fg 16.27
Austrocylichna lagena, 949
Austrocypraea, 780, 783, 784
 affinities, 784
 shell collecting threat, 76
Austrodoris, 941
Austrodoris kerguelensis,
 Fg 16.16
 nervous system, Fg 16.16
Austrodrillia, 848
 endemism, 850
Austroginella
 boring, 839
 endemic, 841
 shell, 838
Austroginella johnstoni
 external appearance, Fg 15.167
Austroginella muscaria
 shell, Fg 15.167
Austroginella tasmanica, Pl 28
Austroharpa, 838
 diversity, 837, 838
 Tertiary, 101
Austroharpa punctata
 shell, Fg 15.166
Austrolima, distribution, 268
Austroliotia, 673
Austromactra, 337
 as fossils, 339
Austromitra, 843–845
 egg capsules, 635, 844
 as fossils, 843, 845
Austromitra analogica
 shell, Fg 15.171
Austromitra rubiginosa, 843
 morphology, Fg 15.171
Austromytilus, endemism, 253
Austromytilus australis
 habitat, 253
Austromytilus rostratus
 habitat, 251
Austroneaera, 425
Austropeplea, 62, 64, 1070, 1071
 affinities, 1071
 in mound springs, 64
Austropeplea lessoni, 1070
 distribution, 64, 83, 1071
 host of avian schistosomes, 64,
 1064
 host of *Trichobilharzia* sp., 69
 radula, 1070
 shell, Fg 17.31
 sperm ultrastructure, Fg 17.19
Austropeplea tomentosa, Fg 1.74,
 66, 67, 69, 70, 1070
 aestivation, 64
 copulatory organ, Fg 17.31
 desiccation, 66
 distribution, 64, 83, 1056, 1071
 economic importance, 66
 host of *Trichobilharzia* sp., 69
 liver fluke vector, 64, 1056, 1071
 radula, Fg 17.31, 1070
 reproduction, 66
 schistosome vector, 1056
 shell, Fg 17.31
Austropeplea vinosa, 83
Austropeplea viridis, 64, 67
Austropyrgus, 755
 distribution, 755
 sculpture, 752
Austropyrgus woodsii
 shell, Fg 15.111
Austrorhytida
 affinities, 1093
 radula, Fg 17.51
Austrorhytida capillacea, 1093
 radula, Fg 17.10
 reproductive tract, Fg 17.51
Austrosuccinea, 85, 1108
Austrosuccinea archeyi, 1108
Austrotindaria wrighti, 239
Austrotriton gibbus
 Tertiary, Fg 1.101
Austrovenus, 358
Austrovenus stutchburyi, 951
 Autobranchia, 225, 249
 autotomy, 1010
 Bivalvia, 219
 Dorididae, 573
 Galeomma takii, 318
 Harpidae, 838
 Limidae, Fg 4.22, 219
 Madrellidae, 1009
 Mourgona, 970
 Prophysaon, 573
 Psammobiidae, 346
 Scaphopoda, 433
 slugs, 1055
 Solecurtidae, 346
 Solenidae, Fg 4.22, 219, 341
 Stomatellinae, 684, 685
 Tellinidae, siphons, 305
 Tethyidae, 1006
Avellana, 946
 Cretaceous, 99
Avicula, eyes, 212
Avicularium, as fossils, 336
Aviculopecten
 Devonian, Tb 1.6
 Permian, 97
 Aviculopectinoidea, 275
Avrainvillea nigricans, 971
Axinopsida serricata
 bacteriocytes, Fg 8.2
 ctenidial microstructure, Fg 8.2
 density, 315
Axius plectorhynchus, 318
Azorinus, 346

Babelomurex lischkeanus
 shell, Fg 15.156
Babinka, 310
 ancestral role, 310
 as lucinoid ancestor, 310
 origins, 310
 bacteria
 in solemyid larvae, 243
 teredinid ctenidia, 374
 bacterial mats as food, 658
 bacteriocytes
 Fimbriidae, putative, Fg 8.4
 Lucinidae, Fg 8.2, Fg 8.3, 207,
 313
 Lucinoidea, Fg 8.2, Fg 8.5
 Solemyidae, Fg 5.11, 207, 243
 Thyasiridae, Fg 8.2, Fg 8.5
 bacteriosome, Thyasiridae, Fg 8.2
Bactroceras latisiphonatum
 connecting rings, 489
Bactronophorus, habitat, 374
Bactronophorus thoracites
 habitat, 378
 pallet, Fg 8.53
Baculites, Cretaceous, 99
Baculites lechitides
 Cretaceous, Fg 1.100
Badepigrus, 747
Badepigrus pupoides
 female genital system, Fg 15.106
 Baie de Marins, 196
Bakevella, Triassic, 97
Bakevelliidae, 265
Balanetta, 841
Balanus, 992
 baler shell, Pl 28, 833
 ballast mechanisms
 Nautiloidea, 486
 Orthoceroidea, 487
Bamyaniceras, Permian, 97
Bandabyssia, 662
Bankia
 habitat, 374
 pallets, 378
Bankia australis
 cones, Fg 8.54
 gill bacteria, 372
Bankia barthelowi, cones, Fg 8.54
Bankia bipalmulata, cones, Fg 8.54
Bankia campanellata
 cones, Fg 8.54
Bankia carinata, cones, Fg 8.54
Bankia gracilis, cones, Fg 8.54
Bankia johnsoni, cones, Fg 8.54
Bankia nestalia, cones, Fg 8.54
Bankia nordi, cones, Fg 8.54
Bankia rochi, cones, Fg 8.54
Bankivia, 671, 689
 craftwork, 672
 distribution, 689
 habitat, 672, 680
 shell, 689
 suspension-feeding, 623
 Tertiary, 101
Bankivia fasciata
 craftwork, 690
 neck lobe, Fg 15.68
 radula, Fg 15.68
 on sand plains, 38
 shell, Fg 15.68
Bankivia howitti, as fossils, 690
Bankiviini, shell, 689
 Banks, Sir Joseph, 6
 Banksian region, 593
 Baptozoididae, 997
Barbatia, 254, 256
 distribution, 256
 diversity in Australia, 256
 as fossils, 256
 habitat, 256
 heart, 256
 hinge, 254
 nestling, 254
 photoreceptors, 212
 sculpture, 254
 shell, 254
Barbatia cf. helblingii
 shell, Fg 6.2
Barbatia fusca, 256
Barbatia helblingii, 256
Barbatia pistachia, endemic, 256
Barbatia squamosa, endemic, 256
Barbatia virescens
 as prey, Fg 15.142
Barleeia, 746, 747
 oesophageal pouches, 746
 operculum, Fg 15.105
 radula, Fg 15.105
 shell, Fg 15.105, 746
Barleeia unifasciata, 746
 head-foot, Fg 15.105
Barleeidae, Fg 15.105, Tb 15.1, 745
 family treatment, 746
 barnacles, as muricid prey, 823
Barnea, 375
 shell/body relationship, Fg 4.10
Barnea australasiae
 distribution, 374
 external appearance, Fg 8.47
 shell, Fg 8.47
Barnea dilatata
 external appearance, Fg 8.47
 shell, Fg 8.47
 siphons, Fg 8.46
Barnea obturamentum, Pl 16
 distribution, 374
 external appearance, Fg 8.47
 shell, Fg 8.47
Barycypraea, as fossils, 784
Baryspira, Tertiary, 101
 basal lobes, Coleoidea, 466
 basal plate, Acmaeoidea, 648
Basilissa, 692
Basilomya, 274
Basilomya goreau, 274
 basins, sedimentary, Fg 1.95
 basket clams, 363
 Basommatophora, 1037, 1047
 description, 1067
 external characters, 1041
 as fossils, 1057
 gut structure, 586
 kidney, 1045
 Bass Basin, Fg 1.95
 Bass Strait
 Aplacophora, 145
 effect of closure, 77
 Neomenia, 157
 Triphoridae, 810
Bassethullia, 165, 188
Bassethullia glypta, 188
Bassethullia matthewsi, Pl 9, 188
Bassethullia porcina, 188
Bassethullia propeporcina, 188
Bassina, 358, 360
 habitat, 358
 Tertiary, 101
Bassina disjecta, 359
 painting, Fg 1.7

INDEX

- Bassina jacksoni*, 357
Bassina pachyphylla, 357
Bassina sensu stricto
 endemic subgenus, 357
Bassleroceratidae, 487
Bassotrochus, Devonian, 95
Basterotia, distribution, 322
Batavia, 6
 bathers itch, 69
Bathmoceras, 489
Bathothauma lyromma
 adult, Fig 1.54
 external appearance, Fig 13.28
 larva, Fig 1.54
Bathoxiphus, 434, 444
Bathoxiphus colmani, 444
Bathoxiphus tricarinarum, 444
 shell, Fig 10.19
Bathraspira, Cretaceous, 99
Bathurst, 7, 196, 919
Bathyacmaea, 646
Bathyarcha, 254
 habitat, 256
 sculpture, 254
 shell, 254
Bathyarcha perversidens
 distribution, 256
 endemic, 256
Bathyberthella, 979
Bathyberthella antarctica, 980
Bathycorbis, 315
Bathycorbis despecta
 distribution, 315
Bathycorbis percostata
 distribution, 315
 shell, Fig 8.4
Bathydoridoidea, 990
Bathymodiolinae, 250
Bathypelta, 656
Bathypelta pacificum, 656
 external appearance, Fig 15.43
 shell, Fig 15.43
Bathyphytophilidae, Fig 15.48,
 Fig 15.50, 658
Bathyphytophilus, 658
 brooding, 654
Bathypolypodinae, 549
Bathysciadiidae, Fig 15.43,
 Fig 15.44, Tb 15.1
 in Australia, 656
 family treatment, 656
 food, 656
Bathysciadium, 656
 radula, Fig 15.43
Bathysciadium aff. costulatum
 protoconch, Fig 15.44
Bathysciadium conicum
 internal morphology, Fig 15.43
Bathysciadium costulatum, 656
Bathyteuthidae, Fig 11.10, Fig 13.19
 family treatment, 530
Bathyteuthis, 530
 external appearance, Fig 11.10
 fin shape, Fig 11.10
Bathyteuthis abyssicola
 external appearance, Fig 13.19
 radula, Fig 13.19, 530
 tentacular club, Fig 13.19
Bathytoma atractoides
 columella, 848
Bathytormis radiatus, 326
Batillaria, 720–722
Batillaria australis, Fig 1.48, 721
 as fossils, 722
 host of *Austrotilharzia*
terrigalensis, 69
 in mangroves, 45
 shell, Fig 15.90
 shell polymorphism, 722
 trematode infections, 722
Batillaria estuarina
 central tooth, Fig 15.90
 shell, Fig 15.90
Batillaria zonalis, 722
 alimentary tract, Fig 15.90
 buccal region, Fig 15.90
Batillariella, 721
Batillariella estuarina, 720, 721
 as fossils, 722
Batillariidae, Fig 1.48, Tb 15.1
 affinities, 718, 724, 732
 characters, 720
 euspermatozoa, 708
 family treatment, 720
 as parasite hosts, 721
Batillariinae, 724
 euspermatozoa, 708
Batissa, 354
 habitat, 61
 hinge, Fig 8.35
 in middens, 355
 pedal gape feeding, 354
 shell, Fig 8.35, 352
 size, 353
 teeth, 353
Batissa violacea, 354
 distribution, 61
 bat-wing slugs, Pl 33, 952
 Baudin, Nicholas, 6, 196, 568, 919
Baudinella regia
 shell, Fig 17.69, 1112
Bayardella
 copulatory organ, 1072
 distribution, 84
 Gondwanan origins, 84, 1074
 shell form, 64
Bayardella cosmeta
 tolerance of desiccation, 65
Bayardella johani
 copulatory organ, Fig 17.33
 shell form, 65
Baylea, Permian, 97
Beagle, 7
 beaks
 Architeuthidae, Fig 11.25
 Argonautidae, Fig 11.25
 cephalopod predator studies, 471
 Cephalopoda, 459
 Coleoidea, Fig 11.25
 Histiotteuthidae, Fig 11.25
 Nautilida, 493
 Nautilidae, Fig 11.25
 Nautiloidea, Fig 11.25
 Octopoda, Fig 11.25
 Octopodidae, Fig 11.25
 Ommastrephidae, Fig 11.25
 Onychoteuthidae, Fig 11.25
 Pholidoteuthidae, Fig 11.25
 Sepiidae, Fig 11.25
 Teuthoidea, Fig 11.25
 Tremoctopodidae, Fig 11.25
 bean cowries, 787
Beania, 1010
Beddomeia, 63, 83
 affinities, 755
 distribution, Fig 1.91, 83
 hydrobiid generic group, 63
 radiation, 82
Beddomeia launcestonensis
 female genital system, Fig 15.111
 shell, Fig 15.111
Bedevea, shell, 823
Bedevea hanleyi, 277
Bedevea, 277
 larval development, 27
 shell, Fig 15.156
 veliger, Fig 1.21
Bedevea paivae
 egg capsules, Fig 1.20, 25
 Bednall, William T., 10, 163
Beguina
 pedal retractor muscles, 323
Beguina semiorbiculata, 324
 distribution, 324
Beguina variegata, 324
 behaviour, 296, 774, 1065
 Anomalodesmata, 402, 403
 Architectonicidae, 862
 Arionidae, 1101
 Assimineidae, 757
 Bithyniidae, 760
 burrowing, Lyonsiidae, 403
 burrowing, Periplomatidae, 403,
 410
Campanile symbolicum, 735
 Cephalopoda, Figs 11.26–11.28,
 471
 Cerithioidea, Fig 15.88
 Columbelloidea, 829
 Conidae, 853
 Cystopeltidae, 1107
 defence, Cephalopoda, 51
 dymantic patterns, Coleoidea,
 Fig 11.27
 Heterodonta, 305
 Limacidae, 1102
 Loliginidae, Fig 11.27
 Naticidae, 790
 Neritidae, 697, 699
 Octopoda, Fig 11.27, Fig 11.28
 Octopodidae, Fig 11.27, Pl 20
Octopus
 Ovulidae, 786
 Palaeoheterodonta, 293
 Planaxidae, 722
 Polyplacophora, 175
 predation, Anomalodesmata, 403
 Psammobiidae, escape response,
 346
 Pulmonata, 1050, 1055
 Pyramidellidae, 867
 Sepiidae, Fig 11.5, Fig 11.26,
 Fig 11.27, 508
 Sepioidea, Fig 11.26, Fig 11.27
 Sepiolidae, Pl 18, 474, 514
 Strombidae, Fig 14.10, 768
 Testacellidae, 1107
 Teuthoidea, Fig 11.27
 Tridacnidae, fish deterrence, 335
 Tridacnidae, righting, 335
 Tridacnidae, spawning 333
 Trochoidea, 672
 Turritellidae, Fig 15.88
 Xenophoridae, 776
 Belcher, Capt. Edward, 7
 Belemnidae, 503
 Belemnoida, Cretaceous, Fig 1.100
Belemnopsis, Jurassic, 97
Bellamyia javanica
 radula, Fig 15.81
 Bellamyinae, 706
Bellastraea, 675
Bellerophon
 Devonian, 95
 Permian, 97
 Silurian, 95
Bellerophonitida, 89
 as cephalopods, 452
 Permian, Fig 1.99
 torsion, 3
Bellerophonitoida, 664
Belloliva
 diversity in Australia, 837
Beloceras, Devonian, 95
Beloteuthis, as fossils, 517
Bembexia, Devonian, 95
Bembicium, 738, 739
 diversity, 739
 ecology, 739
 genetics, 739
 predation by crabs, 739
Bembicium altum, as fossils, 739
Bembicium auratum, Fig 1.48, 739
 in mangroves, 45
Bembicium melanostoma, 739
Bembicium nanum, 26, 27, 739
 age at maturity, 29
 competition, 698
 egg laying, Fig 15.26
 oogenesis, 24
 shell, Fig 15.605
 spawning season, 24
Bembicium vittatum, 739
Benthastelena, in Australia, 686
Benthocardiella, 325
Benthonella tenuis
 larval vertical migration, 637
Benthovoluta, operculum, 825
Benthovoluta claydoni
 distribution, 825
 feeding, 825
 operculum, Fig 15.158
 radula, Fig 15.158
 shell, Fig 15.158
Bentosites, 81
 habitat, 1052
 Bergh, Rudolph, 920
 Bernadinidae, 305, 348
 distribution, 348
 Bernard
 hinge notation system, 200
Bernaya, as fossils, 784
 Bernayinae, 780
 Berry, 499
Berthelinia, 965, 966
 external features, 922
Berthelinia caribbea, 965, 966
Berthelinia limax, 934
Bertheliniinae, 965
Berthella, Fig 16.2, 938, 947, 980
 external features, Fig 16.2
 organisation, Fig 16.1
Berthella medietas, 941, 980
Berthella punctata, 919
Berthella serenitas, 980
Berthella stellata, 941, 980
Berthellina, 980
Berthellina citrina, 938, 980
Berthellinidae, Pl 34
Beshtashella tortilis
 Cambrian, Fig 1.97, 89
Beudanticeras, Cretaceous, 99
Beyrichoceras, Carboniferous, 97
Beyrichoceras mackellari
 Carboniferous, Fig 1.99
Bichoristes, 663, 664
 shell, 664
Bidentaria, hinge teeth, 424
 bilateral symmetry
 Cephalopoda, 451
 bilharzia, 1056, 1072
 biodeterioration
 Bivalvia, 221
 biogeographical patterns
 Australian coast, 593
 biogeographical regions
 Australian marine division, 593
 planktonic organisms, 594
 biogeographical zones
 Australia, 305
 biogeography, 77
 Anomalodesmata, 404
 Aplacophora, 149
 Athoracophoridae, 1110
 Bivalvia, 221
 Cerithiopsidae, 811
 Coleoidea, 502
 Conidae, 853

- conoidean families, 847
Conus, 592
 Cyclophoridae, 704
 freshwater bivalves, 221
 Heterodonta, 305
 Hydromyidae, 989
 larval dispersal, 592
 Nautiloidea, 493
Nautilus, 495
 Octopodidae, 550
 Opisthobranchia, 941
 Ordovician nautiloids, 493
 Palaeoheterodonta, 293
 Pinnidae, 267
 Planorbidae, 1056, 1074
 Polyplacophora, 176
 Pulmonata, 1056
 Pupillidae, 1084
 Pupinidae, 705
 Triphoridae, 811
 Tylodinidae, 978
- bioindicators
 Bivalvia, 221
 freshwater mussels, 60
 Hyriidae, 298
 molluscs, 76
Mytilus, 253
Mytilus edulis planulatus, 221
Saccostrea commercialis, 221
 Unionidae, 293
- biological monitoring
 and Patelloidea, 645
- bioluminescence
Kaloplocamus, 994
Phylliroe, 1006
 Planaxidae, 722, 724
Plocamopherus, 994
- bioluminescent countershading
 Oegopsida, 475
- biomass
 Cephalopoda, 51, 476
- Biomphalaria*
 as schistosome host, 729
- Biomphalaria glabrata*
 as schistosome vector, 1072
- Biomphalaria straminea*
 host of *Schistosoma mansoni*, 70
- Biomphalopa recava*
 radula, Fg 17.56
 shell sculpture, Fg 17.55
- bioturbation, Sareptidae, 240
- Biplex*
 distribution, 801, 802
 as fossils, 802
 protoconch, 802
 Tertiary, 101
- birds
 as molluscan predators, 43
 as solenoidean predators, 341
- Bistolida*, 780
- Bithynia*, 759
 renopericardial system, 745
 suspension-feeding, 623
- Bithynia tentaculata*, 760
 mantle cavity, Fg 15.116
- Bithyniidae, Fg 15.116, Tb 1.4,
 Tb 15.1
 family treatment, 759
 in freshwater, 62, 63, 83
 as hosts of *Clonorchis*, 760
 taxonomic status, 107
- Bittiinae, 709
 sperm storage, 710
- Bittium*, 712
- Bittium*, 733, 799, 811
- Bittium reticulatum*, 54, 55
 head-foot, Fg 15.85
- Bittium sensu stricto*, 712
- Bittium subgranarium*
 as fossils, 712
- bivalve communities, 358
- bivalved gastropods, 964
 Sacoglossa, 962
- Bivalvia, 195
 Aboriginal resources, 195
 alimentary tract, Fg 4.13
 biogeography, 221
 body cavities, 203
 body/shell, Fg 4.10, Fg 4.11
 broadcast spawning, 25
 Cambrian, Fg 1.97
 Cambrian shell features, 223
 Carboniferous, 95
 characters, 5, 12, 195
 circulatory system, Fg 4.15, 210
 classification, 224
 Cretaceous, Fg 1.100, 99
 pallial muscles, Fg 4.5
 description, 195
 Devonian, Fg 1.98, 95
 digestion, Fg 4.13, Fg 4.14, 206
 diversity Ordovician, 92
 ect-aquasperm, 20
 embryology, 216
 evolution, form, Fg 4.5
 evolution, ligament, Fg 4.5
 excretion, 210
 external features and shells, 196
 feeding, Fg 4.12, 5, 206
 fossil history, Tb 1.6, 223
 freshwater, 196
 hinge plate, Fg 4.6
 history of discovery, 195
 in inland waters, 59
 iteroparity, 29
 Jurassic, 97
 larvae, 22
 mantle, Fg 4.8, 203
 mantle folds, Fg 4.8
 monophyletic status, 235
 morphology and physiology, 196
 musculature and locomotion, 204
 natural history, 217
 nervous system, 212
 osphradia, 18
 Permian, 96, 97
 phylogeny, Tb 1.6, 223
 as prey, 219, 825, 832, 833, 836,
 839, 846
 as primary consumers, 219
 radiation and life styles, 224
 reproduction, 24, 214
 respiration, 211
 sense organs, Fg 4.18, 212
 Silurian, Fg 1.98
 siphonal types, Fg 4.8
 Tertiary, Fg 1.101
 Triassic, Fg 1.100
 visceral brain, 18
- black swan
 seagrass consumer, 38
- blackfish
 as hyriid hosts, 293
- blacklip abalone
 fishery, 73, 669
- blacklip oyster, 74
- black-lipped pearl shell, 262
- Blackwood, Capt. Francis, 7
- Blainville, H.M.D. de, 162, 568
- Blake, 431
- Blasicrura*, 780
- Bligh, Elizabeth, 6
- Bligh, William, 6
- blood
 heterodont respiration, 302
 mass in Bivalvia, 210
- blood cockle, 256
- blood flukes, 66
- blood gland
 Cocculinidae, 656
 Opisthobranchia, 929
- blood pressure, 573
 Cephalopoda, 451, 462
 Coleoidea, 501
- blood sinuses
 Cephalopoda, 461
 Opisthobranchia, 928
- blue mussel, Pl 10
 economic importance, 76
 fishery, 76
 mariculture, 76
- blue-ringed octopus
 external appearance, Fg 13.35
 human fatalities, 500, 549
- body axes
 Cephalopoda, 451
 rotation, Coleoidea, 499
 Scaphopoda, Fg 10.2, 431
- body cavities
Aglaja, Fg 16.8
 Aplacophora, 147
 Bivalvia, 203
 Cephalopoda, 457
Chelidonura, Fg 16.8
 Opisthobranchia, Fg 16.8, 925
 Polyplacophora, 164
- body chamber, Nautiloidea, Fg 12.3
- body size
 decrease with depth, 40
- body wall
 Palaeoheterodonta, 290
- Boergesenia*, 974
- Bogasonia*, 947, 948
- Bogia*, 658
- Boissevain, 432
- Bolinus brandaris*
 Tyrian purple, 823
- Bolitaena*, 546
- Bolitaena microcotyla*, 546
 brooding larvae, 546
- Bolitaenidae, Fg 13.32
 family treatment, 546
- Boliteceras*, Cretaceous, 99
- Bollandites*, Carboniferous, 97
- Bolma*, 675
 distribution, 676
 Tertiary, 99
- Bonaparte Basin, Fg 1.95, 88
- Bonartemis*, 360
- Bonellitia*, distribution, 846
- Bonellitia varicifera*
 Tertiary, Fg 1.101
- Bonus*, 656
- Boonea impressa*
 pest species, 867
- Boreopeltis*, Cretaceous, 99
- boring
 accessory boring organ, 622
 Bivalvia, 13, 44, 363
 Buccinidae, 820, 827
 Caenogastropoda, 622
 Capulidae, 583
Capulus, 774
 Cassidae, 583
 Cephalopoda, 459
 Gastrochaenidae, 304, 368
 Gastropoda, 583
 Hiatellidae, 371
 Hiatelloidea, 304, 370
 Jouannetiinae, 376
Leiosolenus, 253
Lithophaga, 253
 Lithophaginae, 221, 253
 Marginellidae, 583, 820, 839
 Martesiinae, 375
 Muricidae, 583, 820, 823
 Myoida, 362
 Mytilidae, 253
 Naticidae, 583, 790
 Naticoidea, 790
 Octopodidae, 549
- Petricolidae, 361
- Pholadoidea, 304, 363, 371, 372
 secretions, 622
- Teredininae, 378
- Tibialectus*, 253
- Tridacnidae, 304, 335
- Vayssiéridae, 583
- Veneridae, 357
- Zonitidae, 583
- boring organ
 Naticidae, Fg 15.134, Fg 15.135
 Naticoidea, Fg 15.134, Fg 15.135
- Borissiakoceras*
 Cretaceous, 99
- Bornella*, 1002
- Bornella anguilla*, Fg 16.87, 926,
 941, 1003
 radula, Fg 16.87
- Bornella stellifer*, Fg 16.87, 1002
 external appearance, Fg 16.87
 swimming, 926
- Bornellidae, Fg 16.87
 diet, 938
 family treatment, 1002
- Borniola*, shell, 318
- Borsoniinae, 848, 850
 Australian genera, 850
- Bosellia mimetica*, Fg 16.49
 external appearance, Fg 16.49
- Boselliidae, Fg 16.49
 family treatment, 968
- Botelloides*, 688, 689
 distribution, 79
 as fossils, 689
- Botelloides bassianus*
 radula, Fg 15.57
 shell, Fg 15.67
- Bothriembryon*, 56, 81, 86, 107,
 1094, 1096
 affinities, 1058
Bulinus gunni, 1058
 diversity, 86
 as fossils, 1058
- Bothriembryon barretti*, Pl 31
- Bothriembryon bulla*
 shell sculpture, Fg 17.53
- Bothriembryon gunnii*, 1096
- Bothriembryon kingii*
 shell, Fg 17.53
- Bothriembryon mastersi*
 reproductive tract, Fg 17.53
- Bothriembryon melo*
 reproductive tract, Fg 17.53
 shell, Fg 17.53
- Bothriembryon praecursor*, 1096
- Bothriembryon spenceri*, 81, 86,
 1096
- Bothriembryon tasmanicus*, 86,
 1094, 1096
 radula, 1095
 shell, Fg 17.53
- Bothriembryonidae, 86
- Bothriembryon praecursoris*
 as fossil, 1058
- Botryllus schlosseri*
 host to *Trivia* eggs, Fg 15.24
- Botula*, 253
 internal morphology, Fg 6.1
- Bouchettriphora pallida*
 feeding, 809
 radula, Fg 15.149
- 'boules' cells
 Cephalopoda, 460
- Boutillieria*, Cretaceous, 99
- Bowen Basin, Fg 1.95
- Bracebridge-Wilson, J., 163
- Brachidontes*, 44
 in seagrass, 39

INDEX

- Brachidontes erosus*
effects of epibiota, 44
habitat, 253
hinge, Fig 6.1
- Brachidontes rostratus*, Pl 10
- Brachidontes ustulatus*
distribution, 223
habitat, 251
- Brachilyrodesma*
Ordovician, Tb 1.6
- Brachiopoda, 5
- Brachioteuthidae, Fig 13.21
family treatment, 532
- Brachiotheuthis*, 532, 537
eggs, 532
orientation, 532
radula, Fig 13.21, 532
- Brachiotheuthis behni*, 532
- Brachiotheuthis cf. picta*
external appearance, Fig 13.21
- Brachiotheuthis picta*, 532
- Brachiotheuthis riisei*, 532
- Brachycycloceras*, 491
- Brachydomoceras*, 491
- Brachyodontes lineata*
cue for settlement, 54
- Brachynephra*, 1060, 1080
- Bradybaena similis*, 1115
distribution, 1115
external appearance, Fig 17.20,
Fig 17.22
jaw, Fig 17.72
pest species, 1055
polymorphism, 1115
radula, Fig 17.72
reproductive system, Fig 17.72
shell, Fig 17.72
Angiostrongylus cantonensis,
1056
- Bradybaenidae, Fig 17.20,
Fig 17.22, Fig 17.72, Tb 1.5,
1113
family treatment, 1115
- Bradybaeninae
distribution, 1115
- bradycardia, Bivalvia, 211
- Brahmaites*, Cretaceous, 99
- brain
Cephalopoda, 465
Vampyroteuthidae, 543
- brain structure
Coleoidea, 466
Nautilus, 465
- branchial cordon
Patellogastropoda, 640
- branchial eye, 281
- branchial hearts, Coleoidea, 463
- Branchiopulmonata, 1067
- Bransonia*, Ordovician, 93
- Brazier, John William, 8, 196, 432,
499, 568, 1038
- Brazierista*, 1093
- breathing tubes
Cyclophoridae, Fig 14.18
Gastropoda, Fig 14.18
Pupinidae, Fig 14.18
- Brechites*, 405, 413–415
ligament, 413
musculature, 205
shell, 413
tube, 414
- Brechites australis*, 405
as fossils, 415
- Brechites novaezelandiae*
distribution, 415
- Brechites penis*
distribution, 415
shell form, Fig 4.2, 199
- Brechites philippinensis*
distribution, 415
- Brechites vaginiferus*
anatomy, Fig 9.12
distribution, 415
shell, Fig 9.11
- Brechites veitchi*, 405
distribution, 415
as fossils, 415
- breeding cycles
environmental variables, 23
Zonitidae, 1104
- breeding season
Abralia andamanica, 521
Anomiidae, 281
Arcidae, 256
Arionidae, 1101
Brachioteuthidae, 532
Camaenidae, 1052, 1113
Chiroteuthidae, 537
Ctenopterygidae, 531
Cypraeidae, 783
Cystopeltidae, 1107
Donacidae, 347
Gastrochaenidae, 368
Helicidae, 1113
Hyriidae, 292, 293, 298
Limaecidae, 1102
Mesodesmatidae, 339
Milacidae, 1103
Octopodidae, 549
Onychoteuthidae, 524
Pinnidae, 266
Pteriidae, 262
Rhytididae, 1091
Scaphopoda, 437
Siphonariidae, 1068
Smeagolidae, 1063
Thysanoteuthidae, 533
Vampyroteuthidae, 543
Velesunio ambiguus, 293
Zonitidae, 1104
- Bremer Basin, Fig 1.95
- Brevinucula*, 237
- Breweriaceras*, Cretaceous, 99
- broadcast spawning
Vetigastropoda, 25
- brooch clams, 293
- brood cannibalism
Calyptraeidae, 773
- brooding, 1100
Anomalodesmata, 401
Argonautidae, Pl 21, 453, 554
Bivalvia, 25
Bolitaenidae, 546
Caenogastropoda, Fig 15.25,
Fig 15.28
Calyptraeidae, 591, 773
Capulidae, Fig 15.28, 774
Carditidae, 324
Carditoidea, 322
Cephalaspidea, 936
Cephalopoda, 22
Cerithioidea, Fig 15.91, Fig 15.94,
708
Chitoninae, 185
Cocculiniformia, 654
Coleoidea, 501
Condylocardiidae, 325
Coralliophilinae, 823
Corbiculidae, 354
Corbiculoidea, 214
Cyamiidae, Fig 8.9, 320
Cyclophoridae, 637
Cypraeidae, 783
Epimeniidae, 148, 156
Fissurellidae, 671
Galeommatoidea, 303
Glacidorbidae, 1075
Haloceratidae, Tb 15.1, 772
and hermaphroditism, 214
Hipponicidae, 591, 770, 771
Hydrobiidae, Fig 15.25
- Hydromylidae, 989
- Hyriidae, 292
- Inciirata, 469
- Ischnochitonidae, 183
- Limaecidae, 981
- Liotiinae, 674
- Littorinidae, 739
- Muricidae, 591, 823
- Mytilidae, 251
- Nacellina, 642
- Nassariidae, 831
- Neoleptonidae, 321
- Octopoda, 469
- Octopodidae, Pl 19, Pl 20, 501
- Opisthobranchia, 25, 936
- Ovulidae, 785
- Planaxidae, Fig 15.91, 25, 591,
637, 722, 724
Planaxis sulcatus, Fig 1.19
- Polyplacophora, 25, 173
- prosobranchs, 637
- Pruvotinidae, 148
- Siliquariidae, 720
- Solariellinae, 688
- Sphaeriidae, 303, 355
- Struthiolariidae, 768, 769
- Teredinidae, 374
- Thecosomata, 980
- Thiaridae, Fig 15.94, 637, 727
- Tremoctopodidae, 551
- Trochoidea, 672
- Turritellidae, 716
- Turritellidae, fossil, 716
- Unionidae, 25, 214
- Unionoidea, 214, 292
- Veneridae, 356
- Vermetidae, 779, 780
- Viviparidae, 591, 637, 707
- Volutidae, 835
- brooding, putative
Parilimyidae, 406
- brooding period
Hyriidae, 292
- Brookesena neozelanica*
protoconch, 860
- Brotia*, 82, 729
- Brotia hainanensis*
as parasite host, 728
- Brotia supralirata*
distribution, 82
- Brown, Robert, 7
- Bryopsis*, 970, 974
- Bryozoa
Beania magellanica, 1010
Bicellaria ciliata, 1010
Bugula dentata, 1010
as corambid prey, 990
as goniodoridid prey, 992
as marginellid prey, 839
Mucopetraliella ellerii, 1009
as nudibranch prey, 938
as onchidoridid prey, 992
Orthoscuticella, 1010
Scrupocellaria cf. scrupaea, 993
as zephyrinid prey, 1010
- bubble raft, Janthinidae, 813, 814
- bubble shells, Pl 24, 943
see also Cephalaspidea
- Bucanopsis*, Devonian, 95
- buccal arms
Pneumodermatidae, 986
- buccal bulb, 997, 1001
Aeolidina, 1011
Bornellidae, 1002
Chromodorididae, 1000
Dendrodorididae, 1000
Dorididae, 999
Dotidae, 1004
Hancockiidae, 1003
Phyllidiidae, 1001
Phylliroidea, 1006
Scyllaciidae, 1005
- buccal function
Lymnaeidae, Fig 17.9
Pulmonata, Fig 17.9
- buccal mass
Cephalopoda, 459
Coleoidea, 500
Gastropoda, 582
Helicidae, Fig 17.8
Janthinidae, 813
Octopoda, Fig 11.13
Octopodidae, Fig 11.13
Pulmonata, Fig 17.8, 1037, 1042
Rhytididae, Fig 17.8
- buccal morphology
Amathinidae, Fig 15.187
Heterobranchia, Fig 15.186,
Fig 15.187
Pyramidellidae, Fig 15.186,
Fig 15.187
Pyramidelloidea, Fig 15.186,
Fig 15.187
- buccal pouches, 621
derivation, 621
Littorinidae, 738
- buccal pump
Goniodorididae, 992
Onchidorididae, 992
- Buccinacea, 819
- Buccinidae, Fig 14.16, Fig 14.23,
Fig 14.25, Fig 15.159,
Tb 15.1, 793
familial limits, 820
family treatment, 825
locomotor wave form, 612
on reef slope, 35
on sand plains, 38
shell ornamentation, 614
subfamilies, opinions, 827
temperate origin, 827
- Buccininae, 827
- Buccinulidae, 827
- Buccinulum*, 827
- Buccinum*, 622
egg capsules, 25
mantle cavity, Fig 14.16
predation on bivalves, 622
- Buccinum australis*, 678
- Buccinum punctata*, 827
- Buccinum undatum*
diet, 584
egg capsule, Fig 15.23
egg mass, Fig 15.23
nurse eggs, 635
as predator, Fig 14.23
- Bucconia*, 949
- Buchanoceras*, 491
- Buchia*, Jurassic, 97
- Buchioidea, 275
- Buckland, William, 7
- Bufo naria*, 794, 796
opercular nucleus, 794
- Bugula*, 993, 994
- bulbus aortae, Fig 15.8
- Bulimidae, 759
- Buliminidae, Fig 17.12
- Bulimulidae, Fig 17.23, Fig 17.53,
Pl 31, Tb 1.5, 86
diversity, 85, 86, 107
family treatment, 1094
Gondwanan origins, 1057
- Bulinus*, 759
as schistosome vector, 1072
- Bulinus bidwilli*, 1085
- Bulinus*, 1074
- Bulinus gunni*
affinities, 1058
as fossil, 1058
- Bulla*, 42, 926, 952, 957, 958

- Bulla ampulla*, 957, 958
shell, Fg 16.36
- Bulla angasi*, 958
- Bulla botanica*, 958
- Bulla incommoda*, 949
- Bulla ordinaria*, 949
- Bulla punctulata*, 958
- Bulla quoyii*, Fg 16.11, Fg 16.13,
Fg 16.36, 957, 958
external appearance, Fg 16.36
gizzard plates, Fg 16.13
jaw plate, Fg 16.11
shell, Fg 16.36
- Bulla semilaevis*, 948, 949
- Bulla verrucosa*, 958
- Bullacta*, 954
- Bullacta exarata*, Fg 16.34
shell, Fg 16.34
- Bullactidae*, Fg 16.34
family treatment, 955
- bullettes, Endocera, 489
- Bullia*, 613
locomotion, 574
- Bullidae*, Fg 16.11, Fg 16.13,
Fg 16.36
diet, 937
family treatment, 957
gizzard, 926
gizzard plate, Fg 16.13
jaw plate, Fg 16.11
- Bulliinae*, characters, 830
- Bullina*, 927, 932, 934, 936, 944,
945
organisation, Fg 16.1
- Bullina lineata*, Fg 16.22, Pl 33,
943, 945
evolution, body form, Fg 16.4
external appearance, Fg 16.4,
Fg 16.22
shell, Fg 16.22
- Bullina melior*, Fg 16.22
shell, Fg 16.22
- Bullinidae*, Fg 16.4, Fg 16.22, Pl 33
characters, 943
family treatment, 944
- Bulloidea*, 940
characters, 957
- Bullomorpha*, 940, 977
- buoyancy
Architeuthidae, 527
Argonautidae, 552
Chiroteuthidae, 537
Lepidoteuthidae, 526
Mastigoteuthidae, 538
Opisthoteuthidae, 545
Sepiidae, 507
- buoyancy chambers
Nautiloidea, 485
- buoyancy control
ammoniacal cephalopods, 456
Bathyteuthidae, 457
Carinariidae, 806
Cephalopoda, 453, 454
Coleoidea, 453
Gonatidae, 457
muscular squids, 455
Nautilidae, 455
Nautiloidea, 486
Nautilus, 453
Sepioidea, 455
- Burdikinia*, Devonian, 95
- Burdikinia burdekinensis*
Devonian, Fg 1.98
- Burn, Robert, 920
- burrow habitat
Solemyidae, Fg 5.10
- burrow lining, 368
Periplomatidae, 408
Teredinidae, 376
Thraciidae, 408
- burrowing, 360
adaptations, 943
Anomalodesmata, 403
Arcoidea, 253
Arcticoidea, 348
Astartidae, 328
bivalve musculature, Fg 4.9
Bivalvia, Fg 4.9, 205, 206, 213,
224
Camaenidae, 1113
Cardiidae, 329
Cephalaspidea, 943
Chaetodermomorpha, 150
Chioninae, 358
Clavagellidae, 412, 413
Columbellidae, 829
Corbulidae, 366
Cucullaeidae, 257
Donacidae, Fg 4.9, 347
Dosiniinae, 358
Epitoniidae, 814, 816
Fasciolaridae, 833
Fimbriidae, 314
Glossidae, 352
Glycymerididae, 260
Heterodonta, 219, 302, 305
Hiatelloidea, 370
Latemulidae, 412
Mactroidea, 305, 336
Mallettiidae, 239
Mesodermatidae, 340
Myochamidae, 418
Myoida, 362
Myoidea, adaptations, 363
Nassariidae, 831
naticoid adaptations, 790
Neomenia, 151
Nuculanidae, 240
Nuculidae, 237
Opisthobranchia, 925
Ordovician bivalves, 224
Ovulidae, 836
Palaeoheterodonta, 290
Periplomatidae, 410
Pharidae, Fg 4.9
Pinnidae, 266
Platyodon, mechanism, 364
prosobranchs, 613
Sacoglossa, 962
Scaphopoda, Fg 10.5, 433
Sepiadariidae, 510
Sepiolidae, 511
Solecurtidae, 346
Solemyidae, Fg 5.10, 241
Solenidae, 302
Solenoida, 305, 340
Sphaeriidae, 218
Strombidae, 766
Struthiolariidae, 768
Tellinidae, 343
Tellinoidea, 305, 342
Terebridae, 850
Testacellidae, 1108
Thraciidae, 408
Tonnidae, 803
Trigoniidae, Fg 4.9, 290, 293
Umboniinae, 689
Veneridae, Fg 4.9
Venerinae, 358
Volutidae, 835
Yoldia, 240
- Bursa*, 793, 794
acid and predation, 622
feeding, 794
habitat, 794
opercular nucleus, 794
prey of veligers, 53
- bursa copulatrix
Caenogastropoda, 632
Neogastropoda, 587
- Bursa cruentata*, 794
external appearance, Fg 15.136
- Bursa granularis*, 793, 794
- Bursa lamarckii*, shell, Fg 15.136
- Bursa latitudo*
protoconch, Fg 15.136
- Bursa ranelloides*, 794
- Bursa rhodostoma*, 794
- Bursa verrucosa*, 794
- Bursatella*, 976
- Bursatella leachii*, Fg 16.57, 977
external appearance, Fg 16.57
- bursicles, 630
- Vetigastropoda*, 629
- Bursidae*, Fg 15.136, Tb 15.1, 792
family treatment, 794
siphonal canal, 793
- Bushia*, 408
- Busyconinae*, 832
- 'button shell', 683
- byssal apparatus
Trigoniidae, 295
- byssal attachment
Pterioidea, 261
Pteriomorpha, 249
- byssal bags
Amygdalum, 253
Lioberus, 253
Modiolusia, 253
Musculista, 253
- byssal cocoons, 249
- byssal drifting
Tellinoidea, 304, 342
- byssal gape
Tridacnidae, 333
Tridacnoidea, 332
- byssal gland
Anomalodesmata, 399
Cyamiidae, Fg 8.9
Lyonsiidae, 399
Mytilidae, 251
Pandoridae, 416
Verticordiidae, 399
- byssal notches, *Anomiidae*, 280
- byssal retractor muscles, 319
Arcoidea, 253
Isognomonidae, Fg 6.10
Malleidae, 262
Mytilidae, 251
Pinnidae, 266
Pteriomorpha, 249
- byssal retractor scars
Pulvinitidae, 265
- Byssocardium*, 336
as fossils, 336
as tridacnid ancestor, 336
- Byssopteria*
Devonian, Tb 1.6
- byssus, 261
Anomalodesmata, 399
Anomioidea, 280
Arcoidea, 253
Arcticoidea, 348
Bivalvia, 198
Corbiculoidea, 352
development, 216
Heterodonta, 302
Limopsoidea, 258
Ostreoida, 268
Palaeoheterodonta, 290
- byssus, larval retention, 204, 205
- 
- Cabestana*
head-foot colour, 801
radula, 800
- Cabestana spengleri*, 800
development, 793
egg mass, Fg 15.143
parental care, 793
- Cacheoceras*, 488
- Cacozeliana*, 712
head-foot, Fg 15.85
- Cacozeliana granaria*
development, 712
operculum, Fg 15.85
protoconch, Fg 14.36, Fg 15.85
radula, Fg 15.85
shell, Fg 15.85, 710
- Cadlina*, Fg 16.10, 1000
radular teeth, Fg 16.10
- Cadlina laevis*, 934
- Cadlinella*, 1000
- Cadulus*, Pl 16, 431, 445
as fossils, 437
- Cadulus aberrans*, 434
- Cadulus angustior*, 445
- Cadulus bordaensis*, 445
- Cadulus californicus*
breeding season, 437
- Cadulus infans*, 446
- Cadulus ludbrookae*, 445
- Cadulus occiduus*, 445
- Cadulus quadridentatus*
captacular motion, 433
- Cadulus simillimus*, 446
- Cadulus spretus*, 445
- Cadulus subfusiformis*
captacula, 433
egg detachment, 436
spawning, 436
yolk granules, 436
- Cadulus vincentianus*, 446
depth range, 437
- Cadulus yatalensis*, 446
- Caecidae*, Fg 14.6, Fg 15.117,
Tb 15.1, 746
affinities, 761
family treatment, 761
loss of apex, 572
- Caecinae*, diversity, 763
- Caecum*, 632
distribution, 763
- caecum
Buccinidae, 621
Coleoidea, 500
spiral, *Vetigastropoda*, 605
- Caecum amputatum*
shell, Fg 15.117
- Caecum bipartitum*
head, Fg 15.117
- Caecum corneum*, 762
- Caecum glabrum*
septum formation, Fg 15.117
- Caecum lilianum*
shell, Fg 15.117
- Caecum pulchellum*, 762
- Caecum variegatum*
shell modification, Fg 14.6
- Caenogastropoda*, Fg 15.12,
Tb 14.1, Tb 15.1, 605, 606,
628, 703, 819
affinities, 703
circulation, 624
ctenidial structure, 579
description, 610
egg capsule production, 636
endostyle, 616
eyes, 629
fertilisation, 631
foregut structure, 585
in fossil record, 594
in freshwater, 580
functional kidney, 626
gonoduct, 631
heart, 623
Hypsogastropoda, 610
mantle cavity, Fg 15.7
nerve ring, 628
nervous system, 628
oesophageal glands, 621

- orders, 703
- osphradium, 630
- podocytes, 627
- prey groups, 621
- protandry, 633
- radula, 610
- reproductive morphology, 587
- respiratory flow, 616
- Sorbeoconcha, 610
- sperm dimorphism, 20
- sperm morphology, 634
- status, 567
- veliger, 22
- Cainozoic, 415
 - Buccinidae, 827
 - Carditidae, 322
 - Carditoidea, 322
 - Condyllocardiidae, 324
 - Cymatiinae, 800
 - Ficidae, 798
 - Fissurellidae, 671
 - fossil record, 99
 - Glossidae, 351
 - Glossoidea, 351
 - Hiatelloidea, 370
 - Kelliellidae, 348, 350
 - Malleidae, 264
 - neogastropod radiation, 819
 - Pandoroidea, 415
 - Pandoroidea, 408
 - Pleurotomariidae, 666
 - Ranellinae, 800
 - Scaphopoda, 437
 - Trapeziidae, 348
 - Trigoniidae, 293, 294
 - Trochoidea, 672
 - Turbinidae, 673
 - Turritellidae, 718
 - Vesicomyidae, 348, 351
- Calappidae, terebrid predators, 851
- Calaurops*
 - Ordovician, 92
- calcareous gizzard
 - Philinidae, 937
 - Scaphandridae, 937
- calcareous sponges
 - as aegiretid prey, 995, 996
- calcicoly
 - Helicinidae, 702
 - Hydrocenidae, 701
 - Neritoidea, 694
- calcite, Bivalvia, 202
- calcitic shell structure, Fg 15.32
- calcium
 - and land snail distribution, 57
- Caldukia*, 941, 1009, 1010
- Caldukia affinis*, Fg 16.99, 938, 941, 1010
 - external appearance, Fg 16.99
- Caldukia albolineata*, 941, 1010
- Caldukia rubiginosa*, 941, 1010
- Caledoniella*, 789
 - commensalism, 772
 - family placement, 772
- Calicophoron calicophorum*
 - parasite, *Gyraulus scottianus*, 67
- Caliphylla*, 969, 970
- Caliphyllidae, Fg 14.8, Fg 16.52
 - family treatment, 969
- Callanaitis*, 360
- Callanaitis disjecta*
 - shell sculpture, 199
- Calliclava albolaqueata*
 - radula, 849
- Calliobasis*, 692
- Callionepon*
 - distribution, 1088
- Calliopaea*, 973, 974
- Calliostoma*, 605, 611–613, 615–619, 621, 623, 626, 631, 680, 685, 686
 - alimentary tract, 616, 617
 - associations, 672
 - circulation, 624
 - development, 631
 - diet, 617
 - eyes, 629
 - feeding, 617
 - locomotion, 613
 - nervous system, 628, 629
 - reproduction, Fg 14.28, 631
 - shell, Fg 15.65
 - stomach, 618
- Calliostoma armillatum*, Pl 23
- Calliostoma canaliculatum*
 - radula, Fg 15.65
- Calliostoma ligatum*
 - head-foot, Fg 15.65
- Calliostoma monile*
 - shell, Fg 15.65
- Calliostoma zizyphinum*, 631, 686
 - circulation, 624
 - egg mass, Fg 15.21
 - egg size, 634
 - internal morphology, Fg 15.3
 - nervous system, Fg 15.18
 - organisation, 605
 - spawn ribbon, Fg 15.21
 - stomach morphology, Fg 15.11
 - vascular system, Fg 15.8
- Calliostomatinae, 679
 - description, 685
- Calliotropini, 680
- Calliotropis canaliculata*, 680
- Calliotropis carinata*, 680
- Calliotropis echidna*, 680
- Calliotropis glyptus*, 680
 - radula, Fg 15.61
 - shell, Fg 15.61
- Calliotropis lamellifera*, 680
- Callista*, 360
 - distribution, 360
 - diversity, 360
 - habitat, 358, 360
 - periostracum, 360
- Callista impar*
 - intertidal distribution, 43
 - shore zonation, Fg 1.45
- Callistina*, as fossils, 360
- Callistochiton*, 182, 183
 - Callistochiton angustensis*, 182
 - Callistochiton antiquus*, Fg 3.34, 182, 183
 - Callistochiton broomensis*, 182
 - Callistochiton clenchi*, 182
 - Callistochiton generos*, 182
 - Callistochiton granifer*, 182
 - Callistochiton mawlei*, 173, 182
 - Callistochiton occiduus*, 182
 - Callistochiton recens*, 182
 - Callistochitonidae, 180
- Callistoma*, 625
- Callistoplacinae, 182
- Callocardia*
 - distribution, 360
 - diversity, 360
 - habitat, 358, 360
 - sediment on shell, 357
- Callochiton*, 172, 181, 183
 - intrapigmentary ocellus, Fg 3.20
 - Tertiary, 183
- Callochiton achatinus*, 172
- Callochiton crocinus*, 165, 173, 181–183
- Callochiton elongatus*, 181
- Callochiton gaussi*, 181
- Callochiton klemi*, 181
- Callochiton mayi*, Fg 3.34, 181
- Callochiton rufus*, 181
- Callochiton septemvalvis*
 - aesthetes, Fg 3.17
- Callochitoninae, 181
- Calloplax*, 169
- Calloplax vivipara*, 173
 - metanephridia, Fg 3.15
 - ovoviviparity, 173
- callum
 - Jouannetiinae, 376
 - Martesiinae, 375
 - Pholadidae, Fg 8.45
- Calma*, 938
- Calpurnus*, 784
- Calpurnus verrucosus*, Pl 3, 784
 - brooding, 785
 - host, 786
- Calstevenus*, 437, 444
 - as fossils, 437
- calymma, Scaphopoda, 436
- Calypptogena*, habitat, 350
- Calypptogena magnifica*, 351
 - age at sexual maturity, 351
 - nestling, 351
- Calyptraea*, 773, 774
 - sex reversal, 633
- Calyptraeidae, Fg 15.9, Fg 15.14, Fg 15.126, Tb 15.1, 44, 772
 - endostyle, 616
 - family treatment, 773
 - head region, Fg 15.126
 - locomotor wave form, 611
 - reproduction, 19
- Calyptraeidea
 - suspension-feeding, 623
- Calyptraeidea
 - Australian fauna, Tb 15.1
 - description, 772
 - families, 772
 - head region, Fg 15.126
 - hermaphroditism, 633
- Camaenidae, Fg 1.3, Fg 1.61, Fg 1.93, Fg 1.94, Fg 14.4, Fg 17.3, Fgs 17.18–17.20, Fg 17.69, Fg 17.70, Pl 32, Tb 1.5, 85, 86
 - age at maturity, 1051
 - in arid zone refugia, 110
 - biogeography, 87
 - family treatment, 1112
 - Gondwanan origins, 1057, 1112
 - radiation, 81, 1112
 - range size, 87, 592
 - subfamilies, 1112
- Camaeninae
 - distribution, 85, 1112
 - diversity, 85
- Camaenoidea
 - description, 1112
 - radula, Fg 17.69
 - shell, Fg 17.69
- Cambrian
 - Bivalvia, 223
 - Ellesmerocerida, 487, 489
 - marine transgressions, 90
 - molluscs, Fg 1.97
 - Nautiloidea, Fg 12.9, 485, 489, 493
 - Plectronocerida, 489
 - Pleurotomarioidea, 665
 - Pojetaia*, 306
 - Protactinoceras, 489
 - Protobranchia, 235
- Cambrian Period, 89
- camerae
 - Nautiloidea, Fg 12.3
 - Nautiloidea, 485
 - Oncocerida, Fg 12.4
- cameral deposits
 - Nautiloidea, 485, 486
- camouflage
 - Aeolidae, 939
 - Anomalodesmata, 398
 - cephalopoda, 51
 - Chromodorididae, 938
 - Coleoidea, 500
 - Cuthona kuiteri*, 939
 - egg cowries, Pl 6
 - Glaucus*, 938
 - Goniodorididae, 992
 - Nudibranchia, 573, 938
 - oceanic cephalopods, 51
 - Opisthobranchia, 938, 939
 - Oxynoidae, 963
 - Pinufius rebus*, 1011
 - Prionovolva*, Pl 6
 - Pulmonata, 1039
 - Sepia officinalis*, Fg 11.5
 - silhouette elimination, 51
 - spindle cowries, Pl 26
 - Xenophoridae, 776
- Campanile*, 733–735, 779, 799
 - affinities, 703
 - as fossils, 735
 - habitat, 734
 - Pliocene, 735
 - relationships, 567
 - Tertiary, 101
- Campanile symbolicum*, 733, 735, 737
 - affinities, 733
 - autapomorphies, 733
 - distribution, 735
 - early teleoconch, Fg 15.98
 - Holocene, 735
 - mantle cavity, Fg 15.98
 - operculum, Fg 15.98
 - Pleistocene, 735
 - radula, Fg 15.98
 - shell, Fg 15.98
 - spawn mass, Fg 15.98
 - spermatozoa, Fg 15.98
- Campanile triseriale*, as fossils, 735
- Campanile virginense*
 - as fossils, 735
- Campanilidae, Fg 15.98, Tb 15.1, 708, 733
 - autapomorphies, 733
 - family treatment, 735
- Campanilimorpha, 733
- Campaniloidea, Tb 15.1, 703
 - affinities, 703, 733
 - description, 733
 - shell, Fg 15.99
 - Tertiary radiation, 733
- Campanilopa*, as fossils, 735
- Campeloma*, parthenogenesis, 634
- Campelominae, 706
- Camptochlamys*, Tb 1.6
- Camptonecies*, Cretaceous, Tb 1.6
- Cancellaria sensu lato*
 - distribution, 846
- Cancellaria cooperi*, feeding, 846
- Cancellaria elegans*
 - shell, Fg 15.172
- Cancellaria spirata*, Pl 29
- Cancellaria* (Merica), 846
- Cancellaria* (Nevia)
 - diversity, 846
- Cancellaria* (Sydaphera)
 - diversity, 846
- Cancellariidae, Fg 15.172, Pl 29, Tb 15.1
 - affinities, 845
 - family treatment, 845
 - genera, 846
 - proboscis, Fg 15.172
- Cancellarioidea
 - Australian fauna, Tb 15.1, 703, 819
 - characters, 845
 - description, 845

- Cancilla*
distribution, 842
diversity in Australia, 842
as fossils, 842
- Cancilla filaris*
egg capsule, Fg 15.169
shell, Fg 15.169
- Canculus*, habitat, 680
- Candidula* sp., agricultural pest, 71
- cannibalism
Carinariidae, 806
Fascioliidae, 833
Octopodidae, 549
- Canning Basin, Fg 1.95, 88
- Cantabricanites*, Carboniferous, 97
- Cantharidella*, distribution, 683
- Cantharidinae, 679, 683, 689
- Cantharidini, 683
- Cantharidus clelandi*, eye, Fg 15.19
- Cantharidus pulcherrimus*
spawning season, 23
- Cantharus*, 827
- Cantharus undosus*
operculum, Fg 15.159
shell, Fg 15.159
- cap ears, 684
- cap limpets, 44
- Capistrocardia fragilis*, 370
- Capitellidae, as terebrid prey, 850
- capsule gland, Fg 15.22, 587, 590
prosobranchs, 632
- capsule-moulding gland
Muricidae, 823
Muricoidea, 820
- captacula
Dentaliida, 439
Dentaliidae, Fg 10.1, Fg 10.6
extension, 433
Scaphopoda, Fg 10.6, 431, 433
structure, 433
- Captitonia*, 743
- captive breeding, Cephalopoda, 470
- captive studies
Brachioteuthidae, 532
Idiosepiidae, 514
Ommastrephidae, 533
Sepiolidae, 514
- Capulidae, Fg 15.19, Fg 15.28,
Fg 15.127, Pl 25, Tb 15.1,
772, 868
family treatment, 774
locomotor wave form, 612
suspension-feeding, 623
- Capuloidea, Tb 15.1
description, 774
- Capulus*, 623, 774
boring, 774
feeding, 774
parasitism, 623
parental care, 637
sex reversal, 633
shell, 774
- Capulus australis*, Pl 25
- Capulus sycophanta*, 774
on host, Fg 15.127
shell, Fg 15.127
- Capulus ungaricus*, 774
anatomy, Fg 15.127
brooding, Fg 15.28
echinospira larva, 787
radula, Fg 15.127
- carbonate recycling
holoplanktonic molluscs, 49
- carbonic anhydrase
in shell boring, 622
- Carboniferous
Achatinellidae, 1081
Anomalodesmata, 405
Ctenodontidae, 241
- Fimbriidae, 313
Helicinidae, 702
Heterobranchia, 854
Limidae, 268
Limoida, 267
marine transgressions, 90
molluscs, Fg 1.99
mytilid shell structure, 250
Mytilidae, 249
Orthurethra, 1080
Pectinoidea, 275
Pholadidae, 363
Pinnidae, 267
Ptenoglossa, 808
Pulmonata, 1057
Scaphopoda, 437
Teredinidae, 363
- Carboniferous Period, 95
- Cardiapoda*, characters, 807
- Cardiapoda placenta*
external appearance, Fg 15.146
- Cardiidae, Fg 1.36, Fg 1.41,
Fg 4.2, Fg 4.3, Fg 4.6,
Fg 4.22, Fg 8.15
affinities, 332
ancestry, 336
on coral reefs, 34
family treatment, 328
on reef flat, 35
on sand plains, 38
subfamilies, 331
- Cardilia*, 340
- Cardilia semisulcata*, 340
shell, Fg 8.24
- Cardiliidae, Fg 8.24, 337
family treatment, 340
- cardinal teeth
Bivalvia, Fg 4.4
Heterodonta, 301
Veneridae, Fg 4.4
- Cardiniidae, 305
distribution, 325
- Cardiocardita raouli*
distribution, 324
internal morphology, Fg 8.12
shell, Fg 8.12
- Cardioidea
description, 328
families, 328
leaping, 13
- Cardiola*, Silurian, Tb 1.6
- Cardiomya*, 425
hinge teeth, 424
prey capture, 213
proteolytic enzymes, 424
- Cardiomya pectinata*, 401
development, 401, 425
spawning, 401
- Cardita*, juveniles, 324
- Cardita calyculata*, shell, Fg 8.12
- Cardita crassicosta*, 198
distribution, 324
pallial cavity, Fg 8.12
sculpture, 199, 301
shell, Fg 8.12
- Cardita excavata*, distribution, 324
- Cardita variegata*, distribution, 324
- Cardites antiquata*, 324
- Carditidae, Fg 4.3, Fg 8.12, 322,
350
family treatment, 322
subfamilies, 324
- Carditoidea
affinities, 307
description, 322
- Cardium*, 331
reproduction, 303
sub-tentacles, 213
- Cardium echinatum*
escape response, Fg 4.22
- Cardium edule*, 28
eye structure, 213, 330
larval development, 28
'*Cardium*' muticum, 330
- Cardium tenuicostata*, 328
- carina, Aplacophora, 146
- Carinapex minutissima*
veliger shell, Fg 15.174
- Carinaria*, 807
characters, 807
locomotion, 575
size, 804
- Carinaria cithara*
external appearance, Fg 15.146
- Carinaria cristata*, size, 806
- Carinaria galea*, radula, Fg 15.146
- Carinaria mediterranea*
swimming, Fg 15.5
- Carinariidae, Fg 15.5, Fg 15.146,
Tb 15.1, 613
distribution, 807
family treatment, 806
in plankton, 47
as salp predators, 804
- Carinarioidea, Tb 15.1
affinities, 804
Australian distribution, 804
description, 804
prey, 622
relationships, 703
taxonomy, 804
- Carnarvon Basin, Fg 1.95, 88
- carnivory, 406
body form, 1039
Carinarioidea, 622
Cephalopoda, 15, 452
Conoidea, 847
group radiation, 621
Janthinoidea, 811
Muricoidea, 820
Naticoidea, 790
Neogastropoda, 819
prosobranchs, 621
pulmonates, 15, 1043
Sacoglossa, 961
Scaphopoda, 434
Septibranchia, 219
shell boring, 15
shell reduction, 1039
Tonnoidea, 792
- carp, 62
- Carpentaria Basin, Fg 1.95
- Carpenter, P.N., 162
- carrier shells, Fg 14.4, 776
- Carsellena exquisitus*, 675
- Carswellina*, 675
- cartrut whelk, 823
- caruncle, Zephyrinidae, 1009
- Carychiinae, 1078
- Carychium*, 1078
as fossil, 1057, 1067
- Caryocorbula*, Tertiary, 99
- Caryodes*, 1093
- Caryodes dufresnii*, 1093
external appearance, Fg 17.52
radula, Fg 17.52
reproductive tract, Fg 17.52
- Caryodidae, Fg 17.1, Fg 17.24,
Fg 17.52, Pl 32, Tb 1.5, 86,
1058
endemism, 1057
family treatment, 1093
Gondwanan origins, 86
- cask shells, 802
- Casmaria*, 795
distribution, 796
habitat, 794
- Casmaria vibexmexicana*
radula, Fg 15.143
- Cassidae, Fg 14.23, Fg 15.137,
Pl 27, Tb 15.1, 792
family treatment, 794
- Cassidaria*, Tertiary, 101
- Cassidula*, 1078
genital ducts, 1078
habitat, 1078
- Cassidula angulifera*, Fg 1.47
shell, Fg 17.37
- Cassidula rugata*, Pl 31
- Cassinae, 794
- Cassis*, 612, 794, 795, 798
digestive secretion, 586
habitat, 794
varices, 794
- Cassis cornuta*, 794, 796
as ornament, 794
radula, Fg 15.137
shell collection, 115
- Cassis fimbriata*, protoconch, 797
- Cassis nana*, protoconch, 797
- Cassis tuberosa*
feeding, Fg 15.137
prey capture, Fg 14.23
- Castalia undosa undosa*, 290
- Cataeginae, 679
- cathepsin B, 236
- Catriona*, 1016
- cat's eye, 675
- caudal gland
Arionidae, 1041, 1100
Charopidae, 1041
Cystopeltidae, 1106
Helicarionidae, 1041
Pulmonata, 1041
- Caudofoveata, 2, 149
- Caudofoveatus*, 151
- Caulerpa*, Pl 37, 938, 940,
963–965, 970
and Cyndrobullidae, 947
and Oxynooidea, 962
sacoglossan diet, 938
- Caulerpa brownii*, 963–965
- Caulerpa cactoides*, 964, 965
- Caulerpa geminata*, 964, 965
- Caulerpa longifolia*, 971
- Caulerpa racemosa*, 963, 964, 971
as volvatellid food, 963
- Caulerpa remotifolia*, 964
- Caulerpa scalpelliformis*, 964, 965
- Caulerpa simpliciuscula*, 965
- Cavolinia*, 923, 982
external features, 923
- Cavolinia gibbosa*, distribution, 941
- Cavolinia longirostris*, 982
- Cavolinia tridentata*, 982
as argonaut prey, 552
- Cavolinia uncinata*, Fg 16.12, 982
- Cavoliniidae, Fgs 1.50–1.52,
Fg 16.12, Fg 16.62, Pl 34,
980
family treatment, 982
- Caymanabyssia*, 662
- Caymanabyssia rhina*
shell, Fg 15.45
- Caymanabyssia sinespina*
external appearance, Fg 15.46
- Caymanabyssiinae*, 662
- Cayutoceras*, 491
- Cellana*, 641, 644–647
in Aboriginal middens, 644
characters, 646
Cretaceous, 99, 647
distribution, 646
diversity, 647
in fisheries, 644

INDEX

- habitats, 647
- Holocene, 647
- Pliocene, 647
- radula, Fg 15.34, 646
- shell, 569, 646
- species, 647
- Tertiary, 644, 647
- Tethyan distribution, 644
- Cellana ampla*
 - Eocene, 647
- Cellana analogia*, 647
- Cellana carpentariana*
 - Cretaceous, 645
- Cellana conciliata*, 647
- Cellana howensis*, 647
- Cellana radiata*, 647
- Cellana solida*, 647
 - in Aboriginal middens, 644
- Cellana testudinaria*, 647
- Cellana tramoserica*, Fg 1.24,
 - Pl 22, 30, 31, 644, 647, 698
- breeding season, 24
- commensalism, 32
- competition, 31
- euspermatozoa, Fg 1.17
- homing behaviour, 577
- influence of macroalgae, 30
- in research, 647
- shell, Fg 14.4, Fg 15.36
- Cellana turbator*, 647
 - radula, 646
 - teeth, 646
- cellulase, 364, 773, 1044
 - Gastropoda, 586
 - Pulmonata, 1044
- cellulose digestion
 - Teredinidae, 374
- cementation
 - Ostreina, 268
 - Ostreoida, 268
 - Pectinidae, 277
 - Spondylidae, 278
- Cenoceras*, 491, 493, 495
- Cenozoic, *see* Cainozoic
- central nervous system
 - Cephalopoda, Fg 11.19, 465
 - Nautilidae, Fg 11.19
 - Octopodidae, Fg 11.19, Fg 11.27
- central tooth, 14
- Centralian Region
 - non-marine molluscs, 81
- Centrapala*, 65, 81, 706
 - distribution, 707
 - endemism, 707
- Centrapala lirata*, 707
 - distribution, 65
- Centrocyrtocera*, 489
- Cepaea hortensis*, 57, 58
 - climate and distribution, 57
 - competition, 58
 - oxygen consumption, 1046
 - water loss, Tb 17.1
- Cepaea nemoralis*, 57, 58
 - climate and distribution, 57
 - competition, 58
 - water loss, Tb 17.1
- Cepaea vindobonensis*
 - oxygen consumption, 1046
- Cephalaspidea, 940, 943
 - characters, 943
 - classification, 943
 - diet, 937
 - evolution of body form, Fg 16.4
 - herbivory, 943
 - internal morphology, Fg 16.3
 - relationships, 940
- cephalic eye
 - Philobrya*, Fg 4.16
 - Philobryidae, Fg 4.16
- cephalic retractor muscle
 - Cephalopoda, Fg 11.3
- cephalic shield, 957
 - Acochlidae, 959
 - Acteonidae, 943
 - Aglajidae, 952
 - Athoracophoridae, 1109
 - Bullinidae, 944
 - Cephalaspidea, 943
 - Cylichnidae, 948
 - Diaphanidae, 947
 - Gastropteridae, 952
 - Haminoeidae, 954
 - Haminoeidea, 954
 - Hydatinidae, 945
 - Philinidae, 950
 - Retusidae, 949
 - Ringiculidae, 946
 - Smaragdinellidae, 956
 - Volvatellidae, 962
- cephalic tentacles
 - Choristellidae, 664
 - Cocculinellidae, 663
 - Cocculinidae, Fg 15.42
 - Cocculinoidea, 655
 - Desmopteridae, Fg 16.65
 - Lepetellidae, 659
 - Patellogastropoda, 642
 - prosobranchs, 629
 - Pseudococculinidae, 663
 - Trochidae, Fg 15.20
 - Vetigastropoda, 629
- cephalic water pores
 - Ocythoidae, 552
 - Tremoctopodidae, 551
- cephaloconi
 - Clionidae, Fg 16.69, 988
 - Gymnosomata, 986
 - Notobranchaeidae, Fg 16.67, 987
- cephalocyst
 - pulmonate embryo, 1051
- cephalopedal sinus, 573
- Cephalopoda, 3, 20
 - annual catches, Tb 1.3
 - beaks as food, 656
 - behaviour, 471
 - body cavities, 457
 - Carboniferous, 97
 - carnivory, 15
 - circulation, 461
 - classification, Tb 13.1
 - courtship, 22
 - description, 451
 - Devonian, 95
 - digestive enzymes, 16
 - ecology, 471
 - economic significance, 74, 475
 - egg laying, 22, 51
 - embryology, 469
 - excretion, 463
 - external appearance, shells, 453
 - eye structure, 19
 - feeding and digestion, 457
 - fisheries, 74
 - general features, 12
 - giant nerve fibres, 18
 - history of discovery, 452
 - human consumption, 502
 - ink, 51
 - life history, 470
 - locomotion, 13
 - methods of study, 476
 - morphology and physiology, 453
 - musculature and locomotion, 454
 - natural history, 470
 - nervous system, 18
 - ontogenetic change, Fg 11.7
 - ontogenetic descent, 51
 - origins, 92
 - pelagic molluscs, 49
 - Permian, 97
 - as prey, 51
 - reproduction, 468
 - semelparity, 29
 - sense organs, 465
- cephalopodium, Cephalopoda, 451
- Cephalopyge*, 1006
- Cerastuinae
 - Gondwanan origin, 1086
- cerata, Fg 16.3, Fg 16.20, 18
 - Aeolidina, 923, 1011
 - Dendronotina, 923, 1001
 - Nudibranchia, 990
 - Phestilla lugubris*, Fg 16.20
 - and photosynthesis, 937
 - Sacoglossa, 961
- ceratal glands, 1009
- ceratal pumping, 929
- Ceratomyopsidae, 351
- Ceratophyllidia*, 1001
- Ceratosoma*, 1000
 - Ceratosoma brevicaudatum*, 919, 941
 - egg mass, Fg 1.20
 - Ceratosoma foliatum*
 - function of apertural lip, 571
 - Ceratosoma oblongum*, 919
 - Ceratosoma trilobata*, Fg 16.83, 999
 - external appearance, Fg 16.83
 - secondary gills, Fg 1.15
- Cerberilla*, 1012
- Cerberilla affinis*, Fg 16.103
 - external appearance, Fg 16.103
- Cerberilla incola*, Fg 16.103, 1012
 - radula, Fg 16.103
- Cercaria longicauda*
 - swimmers itch, 1056
- Cercomya*, as fossils, 412
- cerebral gland, Pulmonata, 1048
- Ceresidae, 702
- Ceresinae, 702
- Cerianthus*, 318
- Cerithidea*, 724, 726, 727
 - diversity in Australia, 727
 - as fossils, 727
 - in mangroves, 45
- Cerithidea anticipata*
 - habitat, 727
 - radula, Fg 15.93
- Cerithidea californica*, 726
 - external appearance, Fg 15.92
- Cerithidea cingulata*, habitat, 727
- Cerithidea largillierii*, habitat, 727
- Cerithidea obtusa*, habitat, 727
- Cerithidea reidi*, 727
 - habitat, 727
 - shell, Fg 15.92
- Cerithidea scalariformis*, 724
 - pallial eye, Fg 15.92
- Cerithidea sensu lato*, 726
- Cerithideidae, 724
 - affinities, 718
- Cerithideopsis*, 726
- Cerithiella*
 - affinities, 811
 - habitat, 811
- Cerithiellinae, 811
- Cerithiidae, Fg 14.12, Fg 14.36,
 - Fgs 15.82–15.85, Tb 15.1, 707
- affinities, 712, 718, 730
- in Australia, 712
- on coral reefs, 33
- euspermatozoa, 708
- family treatment, 709
- genera, 712
- habitat, 709
- locomotor wave form, 612
- on reef flat, 35
- reef intertidal shore, 36
- sperm transfer, 632
- Cerithiinae, 709
- Cerithioclava*, 712
- Cerithioderma*, 775
- Cerithioidea, Tb 15.1, 632, 703
 - acrosome, Fg 1.17
 - affinities, 703, 709
 - and Architaenioglossa, 610
 - Australian families, 708
 - characters, 703, 707
 - crystalline style, 621
 - description, 707
 - families removed, 708
 - habitat, 708
 - osphradium, 630
 - renal gland, 627
- Cerithiopsidae, Fg 1.17, Fg 15.150,
 - Pl 24, Tb 15.1, 708
- diversity in New Zealand, 811
- family treatment, 811
- paraspermatozoa, Fg 1.17
- sperm transfer, 632
- Cerithiopsis*, 724
 - as fossils, 727
- Cerithiopsinae, 811
- Cerithiopsis*, 724
 - distribution, 811
 - diversity, 811
 - egg capsule, 635
 - use of proboscis, 622
- Cerithiopsis carrota*
 - shell, Fg 15.150
- Cerithiopsis tubercularis*
 - alimentary tract, Fg 15.150
 - paraspermatozoa, Fg 1.17
 - spermatozeugma, Fg 1.17
- Cerithiopsis tuberculoides*
 - female genital duct, Fg 15.150
- Cerithiopsoida, 808
- Cerithium*, 712
 - as fossils, 712
 - Jurassic, 97
 - locomotion and shape, 575
 - protoconch, Fg 15.83
 - synonymy, 712
- Cerithium citrinum*
 - radula, Fg 15.83
- Cerithium eburneum*
 - spermatophore, Fg 15.82
- Cerithium echinatum*
 - shell, Fg 15.83
- Cerithium moniliferum*
 - reproduction, 712
- Cerithium munitum*, as fossils, 712
- Cerithium muscarum*
 - egg mass, 635
- Cerithium nodulosum*, 712
 - egg mass, Fg 15.84
- Cerithium punctatum*
 - as fossils, 712
- Cermuella*, 71
 - aestivation, 1113
 - as pests, 71, 1114
- Cermuella virgata*, 57, 71
 - pest species, 71, 1055
- Cestoidea, 68
- Cetacea
 - as cycloteuthid predators, 525
 - as loliginid predators, 519
 - as lycoteuthid predators, 520
 - as sepiid predators, 508
- Cetoconcha*, 422
- Cetothrax*, 408, 409
 - diversity, 409
- Chaenocardiola*, Carboniferous, 95
- Chaenomyidae, 405
- Chaetoderma*, 149, 151
 - depth range, 151
 - laboratory maintenance, 145
- Chaetoderma argenteum*
 - distributional changes, 149

- Chaetoderma nitidulum canadense* stenotopy, 149
- Chaetodermatidae, Fg 2.5
family treatment, 151
- Chaetodermomorpha, 2, 151
description, 2, 150
ect-aquasperm, 20
morphology, Fg 2.2
- Chaetognatha
as carinariid prey, 804, 806
as pterotracheid prey, 807
- Chaetomorpha, 969, 972, 974
- Chaetopleura apiculata
lifespan, 174
- Chaetopleurinae, 182
- Challenger, HMS, 8, 145, 196,
236, 310, 431, 452, 499
- Chama, Pl 13, 309
distribution, 309
Miocene, 309
Pliocene, 309
shell cementation, 307
Tertiary, 99
- Chama fibula, distribution, 309
- Chama iostoma, 309
- Chama lamellifera
Tertiary, Fg 1.101
- Chama lazarus, 309
shell, Fg 8.1
- Chama pacifica, 309
shell, Fg 8.1
- Chama ruderalis
distribution, 309
internal morphology, Fg 8.1
shell, Fg 8.1
- Chamaesipho tasmanica, 31
- Chamelea, lateral teeth, 358
- Chamidae, Fg 8.1, Pl 13, 307
family treatment, 307
genera, 309
on reef conglomerate, 36
on reef slope, 35
- Chamoidea, 226
description, 307
- Chamostrea, 397
- Charcotia, 1008, 1009
- Charcotia granulosa, 1009
- Charcotiidae, Fg 16.97, 1007
family treatment, 1008
- Charilda, 859
- Charisma, 688, 689
- Charisma josephi, shell, Fg 15.67
- Charonia, 800
egg capsule, 636
opercular nucleus, 794
radula, 800
- Charonia lampas, 800
head-foot colour, 801
radula, Fg 15.143
shell, Fg 15.142
- Charonia tritonis, 799
distribution, 801
external appearance, Fg 15.142
as predator of *Acanthaster planci*, Fg 1.31
on reef slope, 35
shell collection, 115
- Charopa albanensis
shell, Fg 14.4
- Charopidae, Fg 14.4, Fg 17.3,
Fg 17.10, Fg 17.20,
Fg 17.55, Fg 17.56, Tb 1.5,
85, 86
affinities, 1057
family treatment, 1097
Gondwanan origins, 1057
gonoduct fusion, 1049
importance of limestone, 107
on Lord Howe Island, 114
on Norfolk Island, 114
secondary ureter, 1046
species ranges, 107
- Chatham, HMS, 195
- Chauliodus, 531
- Chaunoteuthis, 516, 524
- checklists
Australian fossil taxa, 594
Gastropoda, 569
marine gastropods, 569
non-marine gastropods, 569
Patellogastropoda, 639
- Cheilea, 770, 771
- Cheilea equestris, shell, Fg 15.123
- Cheiloceras, Devonian, 95
- Chelidonura, Fg 16.4, Fg 16.8,
Fg 16.18, 934, 952
external appearance, Fg 16.4
haemocoel, Fg 16.8
reproduction, Fg 16.18
- Chelidonura adamsii
painting, Fg 1.9
- Chelidonura electra, Fg 16.16
nervous system, Fg 16.16
- Chelidonura hirundinina, 952
- Chelidonura inornata, Fg 16.17,
Pl 33
Hancock's organ, Fg 16.17
'sensory bristles,' Fg 16.17
- Chelidonura pallida, Fg 16.31
external appearance, Fg 16.31
- Chelidonura sandrana
evolution of body form, Fg 16.4
external appearance, Fg 16.4
- Chelodes
Ordovician, 93
Silurian, 95
- Chelodes calceoloides, Fg 3.26
Silurian, 176
- Chelodes whitehousei
Ordovician, 176
- Chelodidae, 177
- Chelycypraea, 780
- chemical defences
Aplysiidae, 573
Dorididae, 573
Liguus, 573
Opisthobranchia, 918
Oxychilus, 573
Pleurobranchidae, 573
- Chemnitz, J.H., 161
- Chemnitzia mariae
shell, Fg 15.186
- chemoreception
Anomalodesmata, 401
Aplysia californica, 932
Bivalvia, 213
Cephalopoda, 468
Conoidea, 847
Gastropoda, 576, 577
Nautilus, 495
Opisthobranchia, 932
Patellogastropoda, 640, 642
Polyplacophora, 171
- Chenu, 568
- Chevallieria
in Australia, 752
distribution, 752
as fossils, 752
- Chevert, 8, 196, 432
- chiastoneury, 1078
- Ellobiidae, 1047
in Gastropoda, 18
Opisthobranchia, 918
Pulmonata, 1047
- Chiazacmea, 639
- Chicoreus
diversity in Australia, 823
- Chicoreus brunneus
shell, Fg 15.156
- Chicoreus cornucervi
radula, Fg 15.157
- Chicoreus damicornis
shell, Fg 14.4
- Chilina, nervous system, 1047
- Chilopoda, sperm dimorphism, 20
- Chimbuities, Cretaceous, 99
- Chione, 358
byssal gland, 356
as prey, Fg 16.14
- Chione (Liophora), nymph, 356
- Chioneryx, 360
- Chionidae, 356
- Chioninae, 356, 358
- Chiroteuthidae, Fg 11.6, Fg 11.9,
Fg 13.24
family treatment, 533
- Chiroteuthis, 533, 537
external appearance, Fg 11.9
photophores, Fg 11.6
- Chiroteuthis calyx
external appearance, Fg 13.24
funnel locking cartilage, Fg 13.24
- Chiroteuthis imperator, 533, 537
radula, Fg 13.24, 537
- Chiroteuthis joubini, 537
- Chiroteuthis picteti, 533, 537
- chitinase, 459, 1044
Pulmonata, 1044
- chitinous armature,
Dendronotina, 927
Notaspidea, 927
- chiton, 2, 187
musculature, Fg 1.13
see Polyplacophora, 2, 161
- Chiton, 161, 187
as human food, 175
- Chiton magnificus, 169
- Chiton aorangi, 185
- Chiton coccus, 182
- Chiton cumingsii
digestive tract, Fg 3.8
- Chiton glaucus, 187
- Chiton magnificus
metanephridia, Fg 3.15
- Chiton pelliserpentis, Fg 1.23
- Chiton stokesii, 175, 186
- Chiton torri, 185
- Chiton tuberculatus, 174, 175, 185,
186
growth, 174
- Chitonellus, 161
- Chitonium simplex
as chiton parasite, 175
- Chitonidae, Fg 1.23, Fg 3.1,
Fg 3.8, Fg 3.9, Fg 3.15,
Fg 3.18, Fg 3.20, Fgs 3.38–
3.40, Pl 8, 163, 180
aesthetes, Fg 3.18
anatomy, Fg 3.9
colouration, 164
extrapigmentary ocellus, Fg 3.20
family treatment, 185
metanephridia, Fg 3.15
- Chitoninae, 185
fossil record, 187
- Chlamydephoridae, 1091
- Chlamydoconcha
dwarf males, 215
- Chlamydoconcha orcutti
mantle, Fg 4.8
musculature, 205
shell, Fg 4.8
- Chlamydoconchidae, Fg 4.8
- Chlamys, 277, 278
byssus, 277
Cretaceous, Tb 1.6
pallial eyes, 213
protandry, 215
swimming, 206, 277
- 'Chlamys' aff. natans, 278
- 'Chlamys' coruscans, 275
- 'Chlamys' natans, 278
- Chloritidae, 86
- Chloritisanax
habitat, 1052
- Chloritisanax banneri
life span, 1052
- Chlorodesmis, 970
- Chondrinidae, Tb 1.5
- Chondrodontidae, 269
- chondrophores, 200
Anomalodesmata, Fg 9.1
Pholadomyoidea, 406
Thracioidea, 407
- Chondropomidae, 606
- Choniocardita (Carditellopsis), 324
- Chorioplacidae, Fg 3.33, 176
family treatment, 180
- Chorioplacina, 180
- Chorioplax grayi, 164, 180
external appearance, Fg 3.33
habitat, 180
valves, Fg 3.33
- Choristella, 610, 613, 663, 664
penis, 632
shell, 664
- Choristella hickmanae, Fg 15.50
alimentary tract, Fg 15.49
- Choristella marshalli, 664
- Choristella nofronii
protoconch, Fg 15.47
- Choristella ponderi, 664
- Choristella tenera
shell, Fg 15.45
- Choristellidae, Fg 15.45,
Fgs 15.47–15.49,
Tb 15.1, 658
family treatment, 663
- Choristidae, 663
- Chosophilina, 951
- Christmas Island, 187, 189
- Achatinellidae, 1080
- Astrosansonia dautzenbergi, 741
- Chrystella islandica, 741
- Discrevinia balba, 741
- Pickworthiidae, 740
- Reynellona natalis, Fg 15.101,
741
- Sansonia kirkpatricki, Fg 15.101
- Sherbornia mirabilis, 741
- Triphoridae, 810
- chromatophores, Fg 11.24, 986
- cephalopod behaviour, 474
- Cephalopoda, Fg 11.4, 451, 454
- Coleoidea, 500
- Loliginidae, Fg 11.4
- Chromodorididae, Fg 1.20,
Fg 14.8, Fg 14.31, Fg 16.10,
Fg 16.18, Fg 16.20,
Fg 16.83, Pl 1, Pl 35, Pl 37,
997, 999
camouflage, 938
defensive glands, Fg 16.20
generic characters, 999
jaw rodlets, Fg 16.83
use of antifedants, 573
- Chromodoris, Fg 16.10, 1000
organisation, Fg 16.1
radular teeth, Fg 16.10
- Chromodoris alternata, Fg 16.18
reproduction, Fg 16.18
- Chromodoris ambiguus, Fg 16, 18
reproduction, Fg 16.18
- Chromodoris annae
euspermatozoa, Fg 1.17
- Chromodoris coi, Pl 37

INDEX

- Chromodoris kuiteri*, Pl 35
Chromodoris sp.
 mating behaviour, Fg 14.31
Chromodoris westraliensis, Pl 1
 chromosome number
 Bosellidae, 968
 Catinellinae, 1109
 Rhodopemorpha, 960
 Succineidae, 1109
 Thiaridae, 729
Chrysostoma
 distribution, 683
Chrystella, 741
Chrystella finckhi, shell, Fg 15.101
Chrystella islandica, 741
Chysallida, shell, 867
Cidarina cidaris, radula, Fg 15.61
 cilia, ctenidial
 Trigonidae, Fg 7.4
 cilia, eulatero-frontal
 Veneridae, Fg 4.12
Venus, Fg 4.12
 'cilia bottles,' 630, 664
 ciliary blocks, bivalve gill, Fg 4.12
 ciliary creeping,
 Opisthobranchia, 925
 ciliary currents
 Buccinidae, Fg 14.16
 Caenogastropoda, Fg 14.16
 Clavagellidae, 414
 Corbulidae, Fg 8.42
 Cucullaeidae, Fg 6.3
 Cyamiidae, Fg 8.9, 320
 Fimbriidae, 314
 Fissurellidae, Fg 14.16
 Glossidae, Fg 8.34
 Laternulidae, Fg 9.10
 Myidae, Fg 8.41
 Myochamidae, Fg 9.14
 Mytilidae, Fg 6.1
 Patellidae, Fg 14.16
 Patellogastropoda, Fg 14.16
 Pulmonata, 1045
 Rastodontidae, Fg 15.104
 Trapeziidae, Fg 8.33
 Vetigastropoda, Fg 14.16
 Yoldiidae, Fg 4.12
 ciliary-feeding, 15
 Struthiolariidae, 768
 ciliary locomotion, 13, 574, 612
 Neomeniomorpha, 151
 Pulmonata, 1042
 ciliary receptors, Scaphopoda, 436
 ciliary tracts
 Anomiidae, Fg 4.12
 Arcidae, Fg 4.12
 ctenidial filaments, Fg 4.12
 Galeommatidae, Fg 4.12
 ciliation, embryo
 Octopoda, 470
 Sepioidea, 470
 Teuthoidea, 470
 Cimidae, Tb 15.1, 865
Cimitaria, Devonian, Tb 1.6
Cimolithium, Cretaceous, 99
Cimomia, 493
 Cretaceous, 99
Cimomia tenuicostata, Fg 12.10,
 99, 493
 Cretaceous, Fg 12.10
Cingulina, shell, 867
 Cingulopsidae, Fg 15.102, Tb 15.1,
 632, 741
 family treatment, 741
Cingulopsis fulgida, 741
 Cingulopsidae, Tb 15.1, 745
 description, 741
 distribution, 741
Cinnelepetra, 700
Cinnelepetra cinnamomea
 distribution, 700
 external appearance, Fg 15.74
Cinnelepetra linguaviverrae
 distribution, 700
Cionella lubrica
 characters, 1081
 feeding, 1081
 habitat, 1082
 distribution, 1082
 locomotory waves, 1042
 radula, Fg 17.41
 shell, Fg 17.41
 Cionellidae, Fg 17.41, Tb 1.5
 family treatment, 1081
 Cionelloidea, description, 1081
Circe, 358
 habitat, 358
 shell, 358
Circe (Fluctiger), 358
Circe (Redicirce), 358
 endemic subgenus, 357
Circe consola, 357
Circe mistura, 357
Circe tumefacta
 intertidal distribution, 43
 shore zonation, Fg 1.45
 Circidae, 356
 Circinae, 356
Circomphalus
 lateral teeth, 358
Circomphalus foliaceolamellosa
 shell, Fg 8.38
 circulation
 Actinocerida, Fg 12.6, 488
 Anomalodesmata, 401
 Aplacophora, 147
 Bivalvia, Fg 4.15, 210
 Cephalopoda, 461
 Coleoidea, 501
 Discosorida, Fg 12.7, 488
 Gastropoda, Fg 14.20, 581
 Heterodonta, 302
 Incirrata, 462
 Mactroidea, 337
 Mollusca, 16
 Myoidea, 363
 Nautiloidea, Fg 11.15, 488
 Octopoda, Fg 11.15, Fg 11.16
 Opisthobranchia, Fg 16.15, 16,
 928
 Palaeoheterodonta, 290
 Polyplacophora, 167
 prosobranchs, 623
 Pulmonata, Fg 17.11, 1044
 Scaphopoda, 16, 434
 Teuthoidea, Fg 11.15, Fg 11.16
 circulation time, Bivalvia, 210
Circulus, 765
Circulus cingulifera
 shell, Fg 15.119
Circulus mortoni, egg capsules, 764
Circulus texanus, 764
 circumoesophageal ganglion
 Helicidae, Fg 17.14
 Lymnaeidae, Fg 17.14
 Pulmonata, Fg 17.14
 Subulinidae, Fg 17.14
 circumoesophageal ring, Fg 16.16
Helix aspersa, 1047
Circumstella, 673
 Cirrata, description, 545
 Cirratulidae, as prey, 937
 cirri
 Opisthoteuthidae, 545
 Vampyromorpha, 542
 Vampyroteuthidae, 542
Cirrobrachium, 533
 Cirroctopoda, 452
Cirrocerebrum, Cretaceous, 99
Cirsope, as fossils, 759
Cirsotrema
 distribution, 816
 shell, 814
Cirsotrema transenna
 Tertiary, Fg 1.101
 CITES, 102
Cladophora, 970, 972, 974
Cladophora prolifera, 973
 clams
 Australian catch, 220
Clanculus, 683
Clanculus bertheloti
 parental care, 637
Clanculus floridus, shell, Fg 15.63
Clanculus undatus, Pl 23
Claraia, Triassic, 97
 Clarence-Moreton Basin, Fg 1.95
 Clarke, Rev. William Branwhite, 8
 classification, Cephalopoda
 Tb 13.1, Tb 15.2, 261
 Anomalodesmata, Tb 9.1, 405
 Aplacophora, 149
 Arcoidea, 254
 Australian pulmonate groups,
 Tb 17.4
 Bivalvia, 224
 Cardiidae, 331
 Cephalaspidea, 943
 Cephalopoda, 452
 Coleoidea, 452
 Cypraeidae, 780
 Gastropoda, 566, 567
 Glycymerididae, 260
 Helicidae, 1114
 Heterodonta, 306
 Littorinidae, 738
 Mollusca, 1
 Nautiloidea, 485
 Opisthobranchia, 942
 Palaeoheterodonta, Tb 7.1, 294
 Patellogastropoda, 639
 Petricolidae, 361
 Polyplacophora, 177
 prosobranchs, 606
 Protobranchia, Tb 5.1, 235, 237
 Pteriomorpha, Tb 6.1
 Pulmonata, 1060
 Sacoglossa, 962
 Scaphopoda, Fg 10.1, 432, 438
 taxonomic ranking, 609
 Thiele's system, 606
 Veneridae, 356
Clathrina, 996
 Clathrellinae, 850
Clatrosansonia minuta
 shell, Fg 15.101
 Clausiliidae, apex loss, 572
 Clausilionae, 1086
Clausinella, lateral teeth, 358
Clavagella, 397, 413, 414
 adductor muscles, 413
 ligament, 413
Clavagella australis, 397
 distribution, 415
 internal morphology, Fg 9.12
 ligament, 413
 morphology, 414
Clavagella (Bryopa)
 distribution, 415
Clavagella multangularis
 distribution, 415
 as fossils, 415
 shell, Fg 9.11
Clavagella sensu stricto
 as fossils, 415
Clavagella (Stirpulina)
 distribution, 415
Clavagella torresi
 distribution, 414
 Clavagellidae, Fg 4.2, Fg 9.11,
 Fg 9.12, 398
 calcareous tube, 413
 family treatment, 413
 Clavagelloidea, 226
 description, 412
 origin, 413
 Clavatulinae, 850
Clavocerithium, 712
Clavus, 848
 distribution, 850
Clavus unizonalis
 foregut, Fg 15.175
Clea, species, 820
 Cleidothaeridae, Fg 9.15, Pl 16
 family treatment, 419
Cleidothaerus, 397, 404, 419, 420
 evolution, 420
 fossil record, 420
 gonads, 401
 habitat, 402
 mantle fusion, 398
 pedal retractor muscles, 399
Cleidothaerus albidus, Pl 16, 404,
 419, 420
 distribution, 420
 habitat, 404
 shell, Fg 9.15
Cleidothaerus chamoides, 419
Cleidothaerus maorianus, 419
Cleidothaerus pliciferous, 404
Cleidothaerus pliciferus, 419
 distribution, 420
Cleifdenoceras, 491
 Cleiopecta, 1011
Clementia
 distribution, 360
 habitat, 358
Clementia papyracea, 359, 360
 Clementiidae, 356
 Clementiinae, 356, 360
Clenchiella, 755
 sculpture, 752
Clibanarius chapini, 699
Clio, 980, 982
 ovoviviparity, 49
 shell form, 923
Clio recurva, 982
 Clionae, characters, 982
Clione, 988
 bipolar distribution, 594
 swimming, 575
Clione limacina, Fg 16.9, 936, 985,
 986, 988, 989
 antifeedant, 48
 diet, 584
 swimming, 926
Clionella sinuata
 foregut, Fg 15.175
 Clionidae, Fg 16.9, Fg 16.12,
 Fg 16.69, 986
 family treatment, 988
 Clioninae, 988
 Cliopsidae, Fg 16.68, 986
 family treatment, 988
Cliopsis, 988
Cliopsis krohni, Fg 16.68, 988
 external appearance, Fg 16.68
Clithon, diversity, 695
Clithon oualaniensis, 695
 distribution, 695
 shell, Fg 15.72
Clonorchis sinensis, 70
Clonorchis sinensis, 760
 in Bithyniidae, 760
Clymenia, Devonian, 95
Clypeomorus, 712
 habitat, 709

- Clypeomorus batillariaeformis*, 712
Clypeomorus bifasciata
 alimentary tract, Fg 14.25,
 Fg 15.84
 egg mass, Fg 15.84
 as fossils, 712
 mantle cavity, Fg 15.84
 mantle organs, female, Fg 15.84
 shell, Fg 15.83
Clypeosectidae, 669
Cnesterium, 240
 Cnidaria
 as aeolid prey, 938
 as aeolidinan prey, 1011
 as aplacophoran prey, 2, 147
 as architectonicid prey, 862
 as architectonicoidean host, 859
 as architectonicoidean prey, 858
 as dendronotinan prey, 1002
 as dendronotoidean prey, 938
 as epitoniid prey, 814
 as janthinoidean prey, 811
 as larval predators, 53
 as mathildid prey, 859
 as neomeniid prey, 151
 as ovulid host, 786
 as ovulid prey, 784
 as prey of *Glaucus*, 1015
 cnidosacs, Fg 16.3, Fg 16.20
 Aeolidina, 925, 1011
 Arminidae, 1007
 Hancockiidae, 1003
 coastal marine surveys
 Mollusca, 7
Cobcrephora, 177
Cobcrephora corrugata, 177
Cobcrephora silurica, Fg 3.27, 177
Cobcrephoridae, Fg 3.27, 176, 177
 cobra, Teredinidae, 371
Coccocrater, 656
Coccocrater radiata
 external appearance, Fg 15.42
Coccopigya, 654, 656
Coccopigya barbatula, 656
Coccopigya crenilamina, 656
Coccopigya crinita, 656
Coccopigya hispida, 656
 brooding, 654
 copulatory organ, Fg 15.42
 protoconch, Fg 15.44
 shell, Fg 15.42
Coccopigya oculifera, 656
Coccopigya spinigera
 protoconch, Fg 15.44
Coccopigya viminensis, 656
Cocculina, 632, 649, 656
Cocculina baxteri
 shell asymmetry, 653
Cocculina conica, 656
Cocculina craigsmiti
 whale bone as food, 656
Cocculina pristina
 shell asymmetry, 653
Cocculinella, 663
Cocculinella coercita, 663
 shell, Fg 15.45
Cocculinella kopua, 663
Cocculinella minutissima, 663
 alimentary tract, Fg 15.49
 external appearance, Fg 15.46
Cocculinella osteophila, 663
 protoconch, Fg 15.47
Cocculinellidae, Fgs 15.45–15.49,
 Tb 5, Tb 15.1, 658
 affinities, 663
 family treatment, 663
Cocculinidae, Fg 15.42, Fg 15.44,
 Tb 15.1, 640, 655
 Australian fauna, 656
 family treatment, 656
 wood as food, 656
Cocculiniformia
 Australian fauna, Tb 14.1,
 Tb 15.1, 605
 characters, 653
 diversity, 653
 habitats, 653
 relationships, 605, 610
 respiratory flow, 616
 shell form, 653
 status, 567
Cocculinoidea, Tb 15.1, 664
 affinities, 664
 characters, 655
 distribution, 654
 fertilisation, 631
 hermaphroditism, 633
 relationships, 610
Cochlicella
 agricultural pests, 71, 1114
Cochlicella acuta, Fg 1.77, 71
Cochlicella barbara
 external appearance, Fg 17.71
 plant pest, 71
Cochliolepis parasitica
 commensal, 764
Cochlodesma, 410
 lithodesma, 407
 siphons, 410
Cochlodesma praetenuae, 410
 gonads, 410
 siphons, 408
Cochlostomatidae, 21, 703
Cochlostomatinae, 705
 Cocos (Keeling) Islands
Lambis lambis fishery, 768
Codakia, 314
Codakia punctata, shell, Fg 8.3
Codakia tigerina
 shell sculpture, Fg 4.3
Codium, 968, 974
Codium fragile, 974
Coelocion, 1088
 affinities, 86
 habitat, 1052
Coelocion australis, 1088, 1089
 classification, 1088
 distribution, 1089
 diversity in Australia, 1088
 internal lamellae, Fg 17.48
 protoconch, Fg 17.48
 radula, Fg 17.48
 shell, Fg 17.48
 shell sculpture, Fg 17.48
Coelociontidae, 1088
Coelocyclus, Devonian, 95
Coelodon patulus, 415
 coelom
 Bivalvia, 203
 Coleoidea, 500
 Gastropoda, 581
 Octopoda, 457, 463
 Opisthobranchia, 925
 Sepioidea, 457
 Teuthoidea, 457
 coelomic cavities
 Cephalopoda, Fg 11.12, 457
 Octopoda, Fg 11.12
 coelomoduct, Bivalvia, 203, 211
Coelozone, Devonian, 95
Coenaculum, 817
Coenobitus compressus, 699
Coenochoropa macromphala
 shell, Fg 17.55
Coenochoropa multiradiata
 shell sculpture, Fg 17.55
 coiling parameters
 shell shape, Fg 14.5
 Coleoidea, 452
 biogeography, 502
 description, 499
 economic significance, 502
 fossil history, 503
 history of discovery, 499
 methods of study, 503
 morphology and physiology, 499
 natural history, 502
Colina, 712
 collar muscles
 muscular squids, 455
 collection
 Gymnosomata, 986
 permits, 101, 102, 1059
 Pulmonata, 1058
 techniques, 101
 Thecosomata, 981
Collinista in Australia, 673
Collisella, 639, 651, 652
Collisella mixta, 639
Collisella pelta
 respiration, 625
 'Collisella' *scabra*
 pedal glands, 612
 Colloniinae, 673
 collostyle, Pulmonata, 1043
Colobocephalus, 948
 coloniality, Nassariidae, 831
Colotrachelus, 662
Colotrachelus hestica
 external appearance, Fg 15.46
 colour patterns
 Argonautidae, 552
 Coleoidea, 474
 Loliginidae, Fg 11.27
 Octopodidae, Fg 11.27
 Sepiidae, Fg 11.27
 Sepioidea, 475
 colour polymorphism
 Donacidae, 347
 colouration
 Bivalvia, 203
 Epimeniidae, 156
 Psammobiidae, 345
Colpantyx, Ordovician, Tb 1.6
Colpodaspis, 947, 948
Colpodaspis pusilla, 948
Colpodaspis thompsoni, Fg 16.26,
 948
 external appearance, Fg 16.26
Colpospira, 718
Colpospira runcinata
 shell, Fg 15.88
Colubraria, 793, 827
Colubrariidae, 827
 Columbariinae, 825
Columbarium, Tertiary, 99, 101
Columbarium acanthostephes
 Tertiary, Fg 1.101
Columbarium harrisae
 distribution, 825
 operculum, Fg 15.158
 radula, Fg 15.158
 shell, Fg 15.158
Columbarium hedleyi
 distribution, 825
Columbarium hystriculum
 distribution, 825
Columbarium pagodoides
 distribution, 825
Columbarium spinicinctum
 distribution, 825
Columbella, 827, 829
 distribution, 829
 penis, 829
Columbella mercatoria
 feeding, 829
 gastric shield, 829
Columbella punctata, 827
Columbella rustica
 gastric shield, 829
Columbellidae, Fg 15.160, Tb 15.1
 characters, 827
 family treatment, 827
 locomotor wave form, 612
 prostate gland, 632
 on reef slope, 35
 columella, Calyptraeidae, 773
 columellar folds
 Cerithiidae, Fg 14.12
 Gastropoda, Fg 14.12
 and locomotion, 575
 Pyramidellidae, Fg 14.12
 Terebridae, Fg 14.12
 columellar muscle
 action, 611
 structure and function, 613
Colus gracilis, stomach, Fg 14.25
Colus islandicus, nurse eggs, 635
Coluzea, 825
Coluzea aapta, distribution, 825
Coluzea bimurata, 825
Coluzea distephanotis
 distribution, 825
Coluzea icarus
 distribution, 825
Cominella, 820, 827
 boring, 622, 827
 scavengers, 42
Cominella eburnea
 operculum, Fg 15.159
 radula, Fg 15.159
 shell, Fg 15.159
 commensalism, 774
Acanthopleura granulata, 187
Argonauta, 471
Caledoniella, 772
 Calyptraeidae, 774
 Capulidae, Fg 15.127
 Capuloidea, Fg 15.127
Chiton tuberculatus, 187
 Galeommatidae, 316
 Hipponicidae, 770
 Myochamidae, Fg 9.14, 416
Ocythoe, 471
Ocythoe tuberculata, 552
 Pinnidae and shrimps, 267
 on rocky shores, 32
 Vanikoridae, 772
 Veneroida, 306
 Vitrinellidae, 763, 764
 commercial production
Helix aspersa, 1056
 competition
 Littorinidae, 698, 739
 Neritidae, 698
 on rocky shores, 31
 on tidal flats, 43
Compressidens, 444
Compressidens platyceras, 444
 shell, 446
Compsomyx
 distribution, 360
 sediment on shell, 357
Comus, 358
Conacmea, 639
 concentric coiling
 operculum, Fg 15.6
 Conchifera, 2
 characters, 3
 Rostroconchia, 3
 synapomorphies, 3
 conchin, Pulmonata, 1039
 conchiolin, 12
 Nautiloidea, 485
 Conchoidea, 962

INDEX

- Concholepas*
boring by *Hiatella*, 371
Tertiary, 101
Concholepas concholepas
conservation, 115
Concholepas peruviana
fishery, 823
conditioning, 577
Condylocardia, 324, 325
Condylocardia limaeformis
shell size, 199
Condylardiidae, Fg 8.13, 322
family treatment, 324
predation by opisthobranchs, 325
Condylardiinae, 324, 325
Condyllocina, 325
cone valves
Astartidae, 328
Crassatellidae, 326
cones
Bankiinae, Fg 8.54
Pholadoidea, Fg 8.54
Teredinidae, Fg 8.54
Conueplecta callosa
distribution, 85
Conueplecta microconus
distribution, 85
Confusiscala, Cretaceous, 99
Conicella, shell, 691
Conidae, Fg 1.14, Fg 1.30, Fg 1.36,
Fg 14.6, Fg 14.23,
Fg 15.177, Fg 15.178, Pl 29,
Tb 15.1
animal, Fg 15.177
on coral reefs, 33
family treatment, 852
foregut, Fg 15.178
history of discovery, 852
radular tooth, Fg 15.178
on reef flat, 35
on reef slope, 35
shell collecting, 76, 115
shell resorption, 572
venom composition, 847
venom gland, 852
connecting rings
Nautiloidea, 486, 489
Conocardium
Devonian, 95
Permian, 97
Conodonts
phylogenetic relationship, 5, 6
Conoidea, Tb 15.1, 703, 819, 847
anatomy, Fg 15.173
characters, 846
description, 846
prey capture, 622
radular reduction, 610
Conomitra, 843
Conorbinidae, 850
Conorhytis, Palaeozoic, 645
Conostrioceras, 491
Conotomaria, 666
Cretaceous, 99
consecutive hermaphroditism, 633
conservation, 105
aquatic habitats, 110
arid zone refugia, 110
artesian springs, 111
Australian marine molluscs, 114
Australian non-marine molluscs,
106
captive breeding, 112
current strategies, 112
effects of introduced taxa, 109
extinctions, 107
freshwater molluscs, 107
genetic studies, 107
habitat modification, 107
habitat protection, 112
legislation, 112
Lord Howe Island, 113
Norfolk Island, 113, 114
strategies and priorities, 109
terrestrial habitats, 109
terrestrial mollusc fauna, 107
threatened taxa, 107
threatening processes, 107
Tridacnidae, 305
conservation status
criteria for marine species, 115
freshwater molluscs, 65
Constantia, habitat, 772
Contentalina, 444
continental shelf
marine, estuarine sediments, 39
continental slope
fauna off North West Shelf, 594
control burning
effects on molluscs, 108
control of snails, 72
Conuber, 791
egg mass, 790
reproduction, 790
Conuber incei, 790
Conuber sordidus
external appearance, Fg 15.134
life span, 790
Conus, 846, 850, 852–854
biogeography, 592, 853
as bioindicator, 76
chemoreception, 577
dispersal, 592
distribution, 853
diversity in Australia, 853
foregut, Fg 15.178
fossil record, 854
human injury, 853
imposex, 76
locomotion and shape, 575
osphradium, 577
poison gland, 586
salivary glands, 847
shell dissolution, 572
shell modification, Fg 14.6
shell wall resorption, 852
Conus achatinus, 853
distribution, 852
shell, Fg 15.177
Conus advertex, 854
Conus anemone, Pl. 29, 852, 853
endemic, 852, 854
external appearance, Fg 15.177
as fossils, 854
radula, Fg 1.14
salivary glands, 847
shell, Fg 15.177
Conus austroviola, endemic, 854
Conus catus, 853
Conus clarus, endemic, 854
Conus cyanostoma, endemic, 854
Conus dampierensis, endemic, 854
Conus dorreensis, 852, 853
distribution, 852
endemic, 854
shell, Fg 15.177
Conus ebraeus, 853
Conus flavidus
salivary glands, 847
Conus gabelishi, endemic, 854
Conus geographus, 853
human fatality, 853
predation, Fg 14.23
Conus howelli, 854
Conus imperialis, 853
distribution, 852
radular tooth, Fg 15.178
shell, Fg 15.177
Conus klemmei, endemic, 854
Conus lividus, 853
Conus maculosus, 847
Conus marmoreus, 853
Conus miliaris, growth, 853
Conus minnamurra, 854
Conus nodulosus, endemic, 854
Conus omaria, feeding, Fg 1.30
Conus pennaceus, 955
Conus planorbis
in middens, Fg 1.36
Conus puncturatus, 852
Conus reductaspiralis
endemic, 854
Conus rutilus, endemic, 854
Conus sponsalis, 852
Conus striatus, Pl 29, 853
foregut, Fg 15.178
Conus textile, 853
Conus trigonus, endemic, 854
Conus tulipa, 853
Conus vexillum
salivary glands, 847
Conus vitulinus
in middens, Fg 1.36
Conus 'zebra'
shell collection, 76
Cook, Capt. James, 6, 352, 568,
1038
Cooper Basin, Fg 1.95
Cooperella, distribution, 356
Cooperellidae, 305, 356
Copepoda
as molluscan prey, 806, 807, 836
copepod parasites
Elysia coodgensis, 968
Pneumodermatidae, 986
Copidens, Tb 1.6
Copulabyssia, 662
copulation
Cystopeltidae, 1107
Muricidae, 823
Opisthobranchia, 934
Terebridae, 850
copulatory chain
Aplysiidae, Fg 14.39
copulatory spicules
Lepidomeniidae, Fg 2.8
coquina deposits, Fg 8.16, 330
coral reefs
classification, 34
diversity of molluscs, 33, 34
environments, 33
general features, 33
habitat diversity, Fg 1.27, 33
microhabitats, 34
molluscan associations, 34
zonation, 34
Corallastele
in Australia, 686
Coralliophaga, 348, 349
siphons, 349
Coralliophaga coralliophaga
habitat, 349
shell, Fg 8.32
Coralliophila, 823
egg capsules, Fg 14.33
shell, 823
veliger, Fg 14.35
Coralliophila violacea
protandry, 823
Coralliophilinae, 822
coral reef infauna, 35
Corallorhynchus, 278
corals
as coralliophiline prey, 823
as epitoniid prey, 813, 816
molluscan larval predators, 34
Corambe, 990
Corambe pacifica
effect on prey, 991
Corambella, 990
Corambidae, Fg 16.71, Pl 35, 990
association with Bryozoa, 990
family treatment, 990
Corbicula, 203, 221, 222, 353–355
dispersal mechanisms, 222
distribution, 82
hinge, Fg 8.35
shell, Fg 8.35
shell microstructure, 202
teeth, 354
Tertiary, 353
Corbicula australis
brooding, 61
distribution, 61
pest species, 61
in pipes, Fg 1.69, 72
Corbicula (Corbiculina), 222
Corbicula fluminalis, 354
hermaphroditism, 214
protogyny, 354
sex ratio, 214
Corbicula fluminea, 215, 222, 354
ciliary currents, 314
pest species, 61
population density, 219
protandry, 354
sexual expression, 215
Corbicula ovalina
distribution, 61
habitat, 61
Corbiculidae, Fg 1.69, Fg 4.7,
Fg 8.35, Tb 1.4, 352
family treatment, 353
in inland waters, 59, 61
taxonomic status, 107
as trematode vectors, 355
Corbiculina, 354
teeth, 354
Corbiculina australis
habitat, 354
Corbiculoidea, 352
ancestry, 352
description, 352
Corbula, 366
Corbula adelaidensis, 366
Corbula ephamilla, 366
Corbula macgillivrayi, 366
Corbula monilis, habitat, 366
Corbula rotalis, habitat, 366
Corbula sulcata, 366
Corbula tunicata, 366
Corbula verconis, 366
Corbula vicaria, 366
Corbulidae, Fg 8.42
family treatment, 366
oxygen depletion tolerance, 364
Corbulinae, 366
Corculum, 331, 336
Corculum cardissa
symbiotic algae, 332
zooxanthellae, 330
Coreanoceras, 489
Coreospira, Cambrian, 89
Coriandria, 743
distribution, 743
Corillidae, Fg 17.68, Tb 17.4
family treatment, 1110
Coriocella, 787, 789, 790
radula, 786
Coriophora
diversity in Australia, 811
cornea, Loriginidae, 517
Cornellites, Devonian, Tb 1.6
Cornellites catellus
Devonian, Fg 1.98

- Cornirostra pellucida*
external appearance, Fg 15.179
jaw elements, Fg 15.179
morphology, Fg 15.179
operculum, Fg 15.179
radula, Fg 15.179
shell, Fg 15.179
- Cornirostridae, Fg 15.179, Tb 15.1, 856
family treatment, 856
- Corolla*, 926, 980, 984, 985, 988
- Corolla intermedia*, 985
- Corolla ovata*, Fg 16.64, 985
external appearance, Fg 16.64
- Coryphella*, 1012
- Coryphella salmonacea*, 1012
- Cosa*, 260
as fossils, 261
- Coscinasterias calamaria*, 277
- Cosmetalepas*, 669
- Cosmomya*, Permian, 97
- Costacallista*, habitat, 358
- Costasiella*, 966, 971
- Costasiella formicarius*, 971
- Costasiella illa*, 971
- Costasiella nonotai*, 971, 972
- Costasiella ocellifera*, 971, 972
- Costasiella pallida*, 971, 972
- Costasiella* sp., Fg 16.53
external appearance, Fg 16.53
- Costasiellidae*, Fg 16.53, 969
family treatment, 971
- Costellaria*, 844
- Costellariidae*, Fg 15.171, Tb 15.1, 841
characters, 843
family treatment, 843
- Cotton, Bernard Charles, 10, 196, 301, 432, 499, 569, 1038
- counter-illumination, 529
Enoplateuthidae, 521
Oegopsida, 475
- courtship
Camaenidae, 1055
Cephalopoda, 22, 469
Coleoidea, 501
Limacidae, 1055
Limacoidea, 1050
Limax maximus, 590
Loliginidae, 519
male aggression, 24
Octopodidae, 549
Pulmonata, 24
Sepiidae, Fg 11.26
Sepioidea, 473
Stylommatophora, 590
- cowl
Verticordiidae, Fg 9.5, Fg 9.16
- cowries, 780
- Cox, Dr. James C., 9, 163, 569, 704, 1038
- Coxiella*, 62, 65, 112, 755–756
affinities, 755
distribution, 756
diversity, 112, 756
habitat, 756
habitat preference, 83
head foot, Fg 15.112
Holocene, 756
Pleistocene, 756
saline habitat, 65
shell, 755
- Coxiella pyrrhostoma*
genital system, Fg 15.112
- Coxiella striata*, Fg 1.72, 65, 756
conservation, 112
- Coxiella striatula*
operculum, Fg 15.112
radula, Fg 15.112
shell, Fg 15.112
- Coxiellidae, 755
- Cranchia scabra*, Pl 18
external appearance, Fg 13.28
radula, Fg 13.29, 539, 540
- Cranchiidae, Fg 1.54, Fg 11.6, Fg 11.9, Fg 13.28, Fg 13.29, Pl 2, Pl 18
development, 502
family treatment, 539
subfamilies, 540
- Cranchiinae, Fg 13.28, 540
- Crangon crangon*, 514
- Craspedochiton*, 165, 188
- Craspedoplax*, 188
- Crassatella*, Tertiary, 101
- Crassatella indica*, 326
- Crassatellidae*, Fg 8.14, 325
family treatment, 326
predation by octopuses, 326
- Crassatelloidea
description, 325
families, 325
- Crassatellopsis*, Tb 1.6
- Crassatina*, as fossils, 327
- Crassatina ziczac*, 326
internal morphology, Fg 8.14
- Crassinella*, ctenidia, 326
- Crassispirinae, 850
- Crassitoniella*, 744
- Crassostrea*, 54, 272
alternative hermaphroditism, 215
- Crassostrea amasa*, 272
- Crassostrea angulata*
prodissoconch, Fg 4.21
- Crassostrea gigas*, 80, 273
culture, 75
fishery, 75, 220
hermaphroditism, 214
introduced species, 115
prodissoconch, Fg 4.21
shell, Fg 6.15
State fisheries, Fg 1.80
- Crassostrea tuberculata*, 272
- Crassostrea virginica*, 54
growth, 218
hermaphroditism, 214
prodissoconch, Fg 4.21
pyramidellid parasitism, 867
settlement cues, 54
veliger, 52, 53
- Crassostreinae, description, 272
- Cratena*, 1015
- Cratena lineata*, Fg 16.104
external appearance, Fg 16.104
- Crateninae, Fg 16.104, 1015
- Craterodiscus pricei*, 1061, 1110, 1112
distribution, 1110
pallial complex, Fg 17.68
radula, Fg 17.68
reproduction, Fg 17.68, 1112
shell, Fg 17.68
taxonomy, 1110
- Cratis*, hinge teeth, 260
- Cremnoconchus*, 739
- Crenatula*, 265
- Crenavolva tigris*, Pl 30
- Crenellinae, 250
life styles, 253
- Crenilabium*, 943, 944
- Crepidula*, 44, 623, 633, 773, 774
sex reversal, 633
suspension-feeding, 623
- Crepidula aculeata*, 774
distribution, 774
sex reversal, 587
shell, Fg 15.126
- Crepidula fornicata*
mantle current flow, Fg 15.9, 623
morphology, Fg 15.126
protandry, 19, 23
as pyramidellid host, 867
radula, Fg 15.126
reproduction, 19
- Crepidula immersa*, 774
- Crepidula walshi*, 774
- Crepipatella*, 774
- Creseidae,
in bottom sediments, 980
pteropod ooze, 49
- Creseis acicula*, 982
distribution, 941
- Creseis chierchiai*, Fg 1.51, Fg 16.62, Pl 34, 982
external appearance, Fg 16.62
- Creseis virgula*, Fg 16.62, 982
shell, Fg 16.62
- Cretaceous, 97, 271, 825
Aviculopectinoidea, 275
Camaenoidea, 1112
Capulidae, 774
Cardioidea, 328
Carditoidea, 307
Cerithioidea, 707, 708
Conoidea, 847
Crassatelloidea, 326
fossil molluscs, Fg 1.100
Helicoidea, 1113
Hiatelloidea, 370
land snails, 1058
marine transgressions, 91
Monotoidea, 275
Muricoidea, 820
Nautiloidea, 491, 493
Neogastropoda, 610, 819
Patellogastropoda, 645
Pectinoidea, 275
Ringiculoidea, 946
Scaphopoda, 437
Tonnoidea, 794
- Cribrarula*, 780
- Cricophorus nutrix*, 1012
- Crimora*, 993, 994
- Crioceras ammonoides*
Cretaceous, Fg 1.100
- Cristilabrum*
distribution, Fg 1.94
- Cristilabrum bubulum*
distribution, Fg 1.94
- Cristilabrum buryillum*
distribution, Fg 1.94
- Cristilabrum grossum*
distribution, Fg 1.94
shell, Fg 17.69, 1112
- Cristilabrum monodon*
distribution, Fg 1.94
- Cristilabrum primum*
distribution, Fg 1.94
- Cronia*, 822, 823
egg capsule, 823
- Cronia contracta*,
egg laying, Fg 15.26
egg masses, Fg 15.26
- crop juice, Pulmonata, 1043
- Crossata californica*, aperture, 793
- crossed-lamellar layer, Fg 4.7, Fg 15.32, 570
- Crosseola*, radula, 691
- Crosseola concinna*
radula, Fg 15.69
- Crosslandia*, 1005
- Crucibranchaea*, 987
- Crucibulum*, 774
as pyramidellid host, 867
sex reversal, 633
- cruciform muscle scars
Tellinidae, 343
- cruciform muscles
Donacidae, Fg 8.32, 347
Psammobiidae, 345
Solecurtidae, 346
Tellinidae, Fg 8.27, Fg 8.28
Tellinoidea, Fg 8.27, 206, 342
- Crustacea
as molluscan prey, 209, 423, 495, 823, 829, 838, 1002
as molluscan predators, 39, 437
- crypt cells, Nuculidae, 209
- cryptic colouration,
Corambidae, 991
Rathousiidae, 1065
- Cryptobranchia, 997
Nudibranchia, 990
- Cryptochiton*, 175
- Cryptochiton porosus*, 188
- Cryptochiton stelleri*, 161, 164, 167, 175, 188
as human food, 175
lifespan, 174
- Cryptochitoninae, 188
- Cryptoconchus porosus*, 164, 172, 188
spawning, 188
- Cryptodonta, 225, 235
origin, 223
- Cryptomya*, 363, 364
shell, Fg 8.41, 363, 364
- Cryptomya californica*
commensalism, 364
internal morphology, Fg 8.41
siphons, 364
- Cryptomya elliptica*, 364
shell, Fg 8.41
- Cryptonemiales
substrata for limpets, 644
- Cryptopecten vesiculosus*, 275
- Cryptoplacidae, Fg 3.42, Pl 9, 164
family treatment, 189
- Cryptoplax*, 161, 164, 189
- Cryptoplax burrowi*, 189
- Cryptoplax iredalei*, 189
- Cryptoplax larvaeformis*, 189
- Cryptoplax mystica*, 170, 189
spawning, 173
- Cryptoplax royana*, 189
- Cryptoplax striata*, Fg 3.42, Pl 9, 189
- crystal sac, Fg 15.22
Neritidae, 697
- crystalline style, Fg 4.13, 15
action in bivalves, 209
Anomalodesmata, 399
Bivalvia, 209
Caenogastropoda, 621
Corbulidae, 366
Gastropoda, 585
Heterodonta, 302
Myoidea, 364
Mytilidae, 251
Nuculanidae, 209
Orbistellidae, 858
- Ctenamussium thetidis*, 278
- ctenidia, Fg 1.15, 17, 261, 277, 314, 333, 362
see also gills
Anomalodesmata, 399, 400
Anomioidea, 280
Aplacophora, 146
Arcoida, 253
Arcticoidea, 348
bivalve organisational grades, 208

- Bivalvia, Fg 4.1, Fg 4.5, 195, 211
 Cardioidea, 328
 Carditoidea, 322
 Cephalopoda, 464
 Chamoidea, 303
 Coleoidea, 499, 500
 Corbiculoidea, 352
 Crassatelloidea, 303
 Cyamioidea, 303, 318
 eulamellibranchs, Fg 1.15, 303
 Galeommatoidea, 316
 Gazini, 682
 Glossoidea, 351
 heterodont categories, 303
 lamellibranch, Fg 4.5
 Limopsoidea, 258
 Mactroidea, 303, 337
 Mollusca, 17
 Muricoidea, 820
 Myoidea, 363, 364
 Neritoidea, 694
 Neritopsina, Fg 15.74
 Nuculanoidea, 239
 Nuculoidea, Fg 5.1
 Ostreina, 268
 Ostreoida, 269
 Palaeoheterodonta, 291
 Pandoroidea, 415
 Pectinina, 275
 Pholadomyoidea, 406
 Pleurotomarioidea, 665
 prosobranchs, 615
 Protobranchia, Fg 1.15, Fg 4.5,
 Fg 5.1, 211, 235
 septibranch bivalves, Fg 1.15
 skeletal rods, 615
 Solemyoidea, Fg 5.1, 241
 suspension-feeding, 616
 Thracioidea, 407
 Tridacnoidea, 332
 Trochoidea, 672
 ultrastructure
 Solemyidae, Fg 5.11
 Veneroidea, 303, 356
 Verticordioidea, 420
Ctenidiacea, 941
 ctenidial bacteria, Lucinidae, 310
 ctenidial filament,
 Lucinidae, 315
 Thyasiridae, Fg 8.5
 Trigonidae, Fg 7.4
 Ungulinidae, Fg 8.6
 ctenidial lamellae
 Mallettiidae, 239
 Solemyidae, Fg 5.11
 ctenidial microstructure
 Fimbriidae, Fg 8.4
 Lucinidae, 311
 Lucinoidea, Fg 8.2
 Thyasiridae, 315
 ctenidial morphology
 Octopoda, Fg 11.18
 Protobranchia, Fg 5.1
 Sepioidea, Fg 11.18
 ctenidial sense organs, 630
 ctenidial septum
 Cuspidariidae, 424
 function, 422, 424
 Poromyidae, 422
 ctenidial terminology
 Bivalvia, 208
 ctenidial type
 Anomalodesmata, 208
 Cuspidarioidea, 208
 Heterodonta, 208
 Palaeoheterodonta, 208
 Poromyoidea, 208
 Pteriomorpha, 208
 ctenidial vessels, Trochidae, 616
 ctenidial-palp association
 Bivalvia, 208
Ctenocardia, 331
Ctenocardia fornicata
 affinities, 331
Ctenocardia imbricatum
 shell sculpture, Fg 4.3
Ctenocolpus, 718
Ctenodonta,
 Ordovician, Tb 1.6, 92
 Silurian, 95
 Triassic, 97
Ctenodontella
 Devonian, Tb 1.6, 97
 Ctenodontidae, 225
 as fossils, 241
 Ctenodontoidea, 225
 Ctenoglossa, Tb 14.1, 610, 703, 808
Ctenoides, distribution, 268
 ctenolium, Pectinidae, 275
 ctenophores, as larval predators, 53
 Ctenopterygidae, Fg 11.6,
 Fg 11.10, Fg 13.20
 family treatment, 530
Ctenopteryx, 530
 external appearance, Fg 11.10
 fin shape, Fg 11.10
 photophores, Fg 11.6, 530
Ctenopteryx sicula
 external appearance, Fg 13.20
 radula, Fg 13.20, 500, 531
Ctiloceras cyclicum
 shell, Fg 15.117
 Ctiloceratinae, 746, 761
 diversity, 763
Cucullaea, 257
 Jurassic, 97
 myophoric flange, 256
 Tertiary, 99
Cucullaea conamera, 257
Cucullaea corioensis
 Tertiary, Fg 1.101
Cucullaea labiata, 257
 distribution, 257
 mantle cavity, Fg 6.3
 shell, Fg 6.3, 256
Cucullaea vaga, 257
 Cucullaeidae, Fg 6.3, 253
 family treatment, 256
Cucumerunio
 distribution, 82, 298
 glochidium, 59
 Kreffian fluvifauna, 81
 Lessonian fluvifauna, 81
Cucumerunio novaehollandiae, 24,
 61, 292, 298
 breeding season, 292
 brooding period, 292
 morphology, 292
 shell, Fg 7.9
 size, 59
 Cucumerunioninae, 59
Cucurbitula, 368, 370
 distribution, 369
 Cudmore, Frank Alexander, 11
 Cultellidae, 341
Cultellus, 341
Cultellus cultellus, 341
 shell, Fg 8.26
 Cumming, Hugh, 8, 162, 196, 337,
 1038
Cuna, 324, 325
 as fossil, 324
Cuna concentrica, 325
Cuna dalli, brooding, 325
Cuna particula, Fg 8.13
Cunanax, 325
Cuneamya, as fossils, 405
 Cuninae, 324
 cunjevoi, as ranellid prey, 800
 Cunningham, Allan, 7, 8, 196
Cupedora sutilosa, shell, 1112
Cupedora sutilosa, shell, Fg 17.69
Cupidoliva nympha
 swimming, 836
Curacoa, 8
 currents
 Carditidae, Fg 8.12
 Clavagellidae, 414
 Corbulidae, Fg 8.42
 Crassatellidae, Fg 8.14
 Cyamiidae, Fg 8.9
 Myidae, Fg 8.41
 Pholadidae, Fg 8.49
 Rastodontidae, Fg 15.104
 currents, respiratory
 Cephalopoda, 465
Curveulima, diversity, 817
 Cusparioidea, 226
Cuspidaria, 397, 424, 425
 distribution, 425
 as fossils, 425
 hinge teeth, 424
 labial palps, 424
 prey capture, 213
 siphonal ganglion, 425
 siphonal tentacles, 424
Cuspidaria alta, shell, 424
Cuspidaria angasi, shell, Fg 9.18
Cuspidaria costellata
 ligament, 424
Cuspidaria cuspidata
 prey capture, Fg 4.22, Fg 9.5
Cuspidaria dorsirecta
 distribution, 425
Cuspidaria exarata,
 as fossils, 425
 shell form, Fg 4.2, 199
Cuspidaria kerguelensis
 distribution, 425
Cuspidaria latesulcata
 distribution, 425
 shell, Fg 9.18
Cuspidaria levifrons
 distribution, 425
Cuspidaria parva, ligament, 424
Cuspidaria pinna
 distribution, 425
 shell, 425
Cuspidaria plicata, 425
Cuspidaria ros
 distribution, 425
 shell, 425
Cuspidaria subrostrata
 as fossils, 425
Cuspidaria trigonalis
 distribution, 425
 shell, 425
 Cuspidariidae, Fg 4.2, Fg 4.22,
 Fg 9.5, Fg 9.18
 family treatment, 424
 origins, 425
 septum, 209
 statocyst, 214
 Cuspidarioidea
 affinities, 424, 425
 description, 424
Cuthona, Fg 16.107, 1016, 1017
 external appearance, Fg 16.107
Cuthona kuiteri, Fg 16.18,
 Fg 16.20, 936, 1016
 cerata, Fg 16.20
 cnidosacs, Fg 16.20
 reproduction, Fg 16.18
Cuthona poritophages, Fg 16.19,
 Fg 16.20, 935-937
 cerata, Fg 16.20
 development, Fg 16.19
Cuthona sibogae, Fg 16.107, Pl 36
 radula, Fg 16.107, 1016
 cuttle, Sepiidae see shell
 cuttlefishes, 505
 fisheries, 74
 Cuvier, George, 639
 Cuvierina, 982
 Cuvierininae, characters, 982
 Cyamiidae, Fg 8.9, 318
 family treatment, 318
 Cyamioidea
 description, 318
 families, 318
Cyamiomactra, 319, 320
 external appearance, Fg 8.9
Cyamiomactra communis
 shell and hinge, Fg 8.9
Cyathodonta, 408
Cycladicama, 315
Cyclidia, as fossils, 695
Cyclina, 360
Cyclinella, 360, 361
 Cyclinidae, 356
 Cyclininae, 356, 360
 Cyclobranchia, 639
Cyclocardia (Vimentum), 324
Cycloclymenia, Devonian, 95
 Cyclocoeliidae, Tb 1.1, 67
Cyclotitites, Silurian, 95
Cyclolobus, Permian, 97
 Cyclomya, 3
Cyclonema, Devonian, 95
 Cyclonoidea, 817
Cyclonoidea carina, 817
Cyclopecten, 278
Cyclopecten favus, 278
 Cyclophoridae, Fg 14.18, Fg 15.78,
 Tb 1.5, Tb 15.1, 628, 703
 buccal pouches, 621
 family treatment, 704
 nervous system, 628
 podocytes, 627
 Cyclophoroidea, Tb 15.1, 567, 610,
 703
 affinities, 703
 description, 703
 families, 703
 on land, 55
 in Palaeozoic, 606
 pallial kidney, 626
Cycloplectoceras, 491
 Cyclostrematidae
 liotine taxa, 673
 Cyclostrematinae, 673
Cyclostremiscus beaulti, 763
 commensal, 764
 protandry, 745, 764
 Cycloteuthidae, Fg 13.15
 family treatment, 525
Cycloteuthis, 525
 mantle, 525
Cycloteuthis akimushkini, 525
Cycloteuthis sirventyi, 525
 external appearance, Fg 13.15
 Cyerce, 969-971
 autotomy, 573
 external appearance, Fg 14.8, 922
Cyerce antillensis, 970
Cyerce cristallina, 970
Cyerce elegans, Fg 16.52, 970, 971
 external appearance, Fg 16.52
Cyerce kikutarobabai, 970, 971
Cyerce nigra, Fg 16.52, 970, 971
 external appearance, Fg 16.52
Cyerce nigricans, 970, 971
 Cygnet, 6
Cylichna, 922, 934, 948, 949
Cylichna alba, Fg 16.4
 external appearance, Fg 16.4

- Cylichna bulloidea*, 949
Cylichna thetidis, Fg 16.10, Fg 16.14, 949
 gizzard plates, Fg 16.14
 radular teeth, Fg 16.10
Cylichnatys, 955
Cylichnatys campanula, 955
Cylichnella bidentata, Fg 16.14
 gizzard plates, Fg 16.14
Cylichnidae, Fg 16.4, Fg 16.10, Fg 16.14, Fg 16.27, 943
 evolution, shell, body, Fg 16.4
 family treatment, 948
Cylichnium, 948, 949
Cylindrinae, 841
Cylindrobulla, Fg 16.25, 961–963
 external appearance, Fg 16.25, 922
 organisation, Fg 16.1
Cylindrobullidae, Fg 16.25
 characters, 947
Cylindrobulloidea, characters, 947
Cylindromitrinae, 841
Cylindrovertilla, 1084
 shell, 1082
Cylindrovertilla hedleyi
 shell, Fg 17.42
 shell sculpture, Fg 17.3
Cyllene lactea, shell, Fg 15.161
Cylleninae, 830
Cymatiidae, 799
 locomotor wave form, 612
 shell ornamentation, 614
Cymatiinae, 799
 characters, 800
Cymatium, 800, 802
 acid in predation, 622
 burrowing, 797
 head-foot colour, 801
 larval life span, 793
 prey of veligers, 53
 radula, 800
 siphonal canal, 793
 as tridacnid predator, 335
Cymatium andamanense
 protoconch, Fg 15.142
Cymatium aquatile
 radula, Fg 15.143
Cymatium gemmatum, 800
Cymatium intermedium, 800
 protoconch, Fg 15.142
Cymatium martinianum
 as pest species, 802
Cymatium mundum, 800
 feeding, 800
Cymatium muricatum
 aperture, 570
Cymatium muricinum, 800
 feeding, 800
 pest species, 802
Cymatium nicobaricum, 800
 feeding, 800
 internal morphology, Fg 14.1
 pest species, 802
Cymatium parthenopeum, 800
 distribution, 800
 feeding, 800
 head-foot colour, 801
 larval life span, 800
 parental care, 793
 predation on oysters, 802
Cymatium pileare, 800, 802
 feeding, 800
 head-foot colour, 801
Cymatium pyrum, shell, Fg 15.142
Cymatopegma, Cambrian, 92
Cymbiola
 distribution, 835
 as fossils, 835
Cymbiola flavicans
 shell, Fg 15.164
Cymbiola pulchra
 regional variation, 36
Cymbiolacca complexa
 radular teeth, Fg 15.164
Cymbium, brooding, 835
Cymbophora, 339
Cymbula, 641, 645
 radula, Fg 15.34
Cymbulia, 926, 984, 985
 shell form, 923
Cymbulia sibogae, Fg 16.64, 985
Cymbuliidae, Fg 16.64, 980
 family treatment, 984
 pseudoconch, Fg 16.64
Cymopolia, prey of *Mourgona*, 970
Cyphoma, 784–786
 as fossils, 786
 oesophageal pouches, 785
Cyphoma gibbosum, 785
 anatomy, Fg 15.131
Cyphoma signatum
 mating behaviour, 786
Cypraea, 612, 780, 783
 dispersal, 592
 internalisation of shell, 573
 protoconch, 783
 shell collecting threat, 76
Cypraea angustata, 780
Cypraea annulus, 783
Cypraea argus, Pl 26
Cypraea armeniaca, 783
Cypraea caputserpentis, 782, 783
 radula, Fg 15.130
Cypraea carneola, 783
Cypraea cervus, 782
Cypraea cf. tigris
 in middens, Fg 1.36
Cypraea comptoni, Pl 26
Cypraea cribraria, Fg 1.33, 782
Cypraea decipiens, 783
Cypraea eglantina, 782
Cypraea erosa, 783
Cypraea friendii, 782, 783
 anatomy, Fg 15.130
 radula, Fg 15.130
 shell, Fg 15.130
 veliger, Fg 15.130
Cypraea gigas, 782
Cypraea helvola, 783
Cypraea hesitata, 783
Cypraea hirasei, 783
Cypraea isabella, 783
 protoconch, Fg 1.58
Cypraea marginata, 783
Cypraea mauritiana, 783
Cypraea minoridens, 782
Cypraea moneta, 782, 783
 distribution, Fg 1.88, 79, 593
 paraspermatozoa, Fg 1.17
Cypraea piperita, 783
Cypraea reevei, 782–784
Cypraea roseli, 783
Cypraea rosselli, distribution, 593
Cypraea spadicea, 782
Cypraea subviridis, 783
Cypraea teres, 782
Cypraea thersites, shell, Fg 15.130
Cypraea tigris, 782, 783
 external appearance, Fg 15.130
 shell, Fg 15.130
Cypraea venusta, 782, 783
 breeding season, 783
 embryo, Fg 15.130
 juvenile, Fg 15.130
Cypraea xanthodon, 783
Cypraecassis, 794, 795
 habitat, 794
 larval dispersal, 796
 prey of veligers, 53
Cypraecassis rufa, 802
 use in jewellery, 794
Cypraecassis testiculus
 egg mass, 793
Cypraedia, Tertiary, 99
Cypraeidae, Fg 1.17, Fg 1.33, Fg 1.36, Fg 1.58, Fg 1.88, Fg 15.130, Pl 26, Tb 15.1, 12
 Australian genera, 780
 on coral reefs, 33
 family treatment, 780
 history of discovery, 780
 locomotor wave form, 612
 on reef crest, 35
 shell collecting, 76, 115
Cypraeinae, 780
Cypraeoidea, Tb 15.1
 description, 780
Cypraeovula, 783, 784
Cypricardella
 Devonian, Tb 1.6
Cypricardiidae, 348
Cypricardinia, Tb 1.6
 Carboniferous, 95
 Devonian, Tb 1.6
 Silurian, Tb 1.6
Cypricardinia minima
 Devonian, Fg 1.98
Cyprinus carpio
 predator on gastropods, 62
Cyrenoida, distribution, 309
Cyrenoididae, 309
Cyrenopsis, Tb 1.6
 Cretaceous, Tb 1.6
Cyrenopsis huddlestoni, Tb 1.6
Cyrenopsis meeki, Tb 1.6
Cyrrilla dalli, 244
Cyrtocera, connecting rings, 489
Cyrtodaria, 370
Cyrtodonta, Ordovician, Tb 1.6
Cyrtodontidae, 253
Cyrtodontula, Tb 1.6
 Ordovician, 92
Cyrtogomphus, Devonian, 95
Cyrtosoma, characters, 3
Cystiscidae, 838
 characters, 839
Cystiscus, 841
 shell, 838
Cystiscus angasi
 external appearance, Fg 15.167
 shell, Fg 15.167
Cystiscus multidentatus, Pl 28
Cystopelta, 1102, 1107
 distribution, 1107
 external appearance, Fg 17.1, Fg 17.64
 feeding, 1054
 radula, Fg 17.64
 water conservation, 1055
Cystopelta astra
 distribution, 1107
Cystopelta bicolor
 distribution, 1107
Cystopelta petterdi
 distribution, 1107
 oviducal pore, 1107
 radula, Fg 17.10
 reproductive tract, Fg 17.64
Cystopelta purpura
 water conservation, 1059
Cystopelta purpurea
 distribution, 1107
Cystopeltidae, Fg 17.1, Fg 17.10, Fg 17.64, Tb 1.5, 86, 1102
 affinities, 1057
 endemism, 1057
 faecal coil, Fg 17.64
 family treatment, 1106
 visceral mass separation, 1039
Cystoseira barbata, settlement, 54

Dacrydiinae, 250
Dacrydium viviparum
 brooding, 251
Dalium, 794
 Dall, J., 639
 Dall, William H., 162, 431
 Daly Basin, Fg 1.95, 88
Damochlora spina
 shell, Fg 17.69, 1112
Damoniella, 956
 Dampier, Capt. William, 6
 Dampierian Province, 593
 Cerithiopsidae, 811
 Dampierian Region, 593
 non-marine molluscs, 81
 dams, effects on mussels, 60
Dana, 542, 546
 Dana, James, 7
Daphnella botanica
 endemic, 848
 shell, Fg 15.174
Daphnellinae, 850
 dart apparatus, 1106
 Helicidae, 1113
 dart sac, 1104
 Helicidae, 1113
 date mussels, in seagrass, 39
Dauchites, Permian, 97
Davainea proglottina
 parasite in poultry, 68
Davaineidae, 68
Davila, 339, 340
Davila plana, shell, Fg 8.23
Davilinae, 340
Dawsonoceras, 491
 de Freycinet, Louis, 196
 de Lamarck, Jean Baptiste, 7
 de Vlamingh, Willem, 6
 Debrachia, 452
 Decapoda,
 euspermatozoa, 20
 spawning, 25
Decatopecten, 278
 swimming, 277
Deceptrix, Tb 1.6
 Ordovician, Tb 1.6, 92
Decorifer, 949, 951
 deep-sea sediments
 molluscs, 40
 defensive behaviour
 Cardioidea, 220
 Galeommatidae, Fg 4.22
 Helicarionidae, 1055
Hexabranhus sanguineus, 998
 Limidae, Fg 4.22
 Pectinoidea, 220
 Pulmonata, 1055
 Sepiolidae, Fg 11.27
 Solenidae, Fg 4.22
 Tremoctopodidae, 551
 Trigoniidae, 220
 defensive chemicals
 Bivalvia, 219
 Galeommatidae, 220

INDEX

- defensive glands
Chromodorididae, Fg 16.20, 999
Dorididae, 998
Titiscaniidae, 701
- defensive structures
Opisthobranchia, Fg 16.20
- Delectopecten*, 277
byssus, 277
pseudo-ctenolium, 275
- Delicatoplax*, 176, 187
- Delicatoplax translucens*, 187
- Deltachion brazieri*
distribution, 347
- Deltodonautilus*, 493
- Deltopecten*, Permian, 97
- Deltopecten farleyensis*
Permian, Fg 1.99
- Deminucula*, 237
- Demospongiae
as notaspidean prey, 937
- Dendostrea*, 272
sculpture, 272
- dendritic gills, 923
- Dendrodorididae, Fg 16.84, 990, 997
family treatment, 1000
prey, 926
- Dendrodoridoidea, 990, 1001
- Dendrodoris*, 1000
- Dendrodoris aurea*, 919
- Dendrodoris citrina*, 1000
- Dendrodoris guttata*, Fg 16.84
external appearance, Fg 16.84
- Dendrodoris limbata*
polygoidal, 573
- Dendrodoris violacea*, 919
- Dendronotina, 990
characters, 1001
external appearance, 923
internal morphology, Fg 16.3
- Nudibranchia, 990
- Dendronotoidea
diet, 938
rhinophores, Fg 16.17
- Dendrophyllia*, 939, 1016
- dendrophylliid corals
as prey of *Phestilla* spp., 1016
- Dendropoma*, 779, 780
operculum, 779
web-feeding, 584
- Dendropoma irregulare*
anatomy, Fg 15.129
- Dendropoma lamellosa*
nucleus, Fg 15.129
radula, Fg 15.129
- Dendropoma maxima*
ciliary feeding, 584
suspension-feeding, Fg 14.24
- Dendropoma squamifera*, 780
- Dendropupa*, as fossil, 1086
- Dendrotina
external features, Fg 16.2
- Dennantia ino*, Tertiary, Fg 1.101
- density
Donax deltoidea, 347
Fragum erugatum, 330
Mesodesmatidae, 340
Tellinidae, 343
Tellinoidea, 342
Tridacnidae, 335
- Dentaliida, 431
description, 439
- Dentaliidae, Fg 1.3, Fg 10.1, Fgs 10.3–10.5, Fg 10.9, Fg 10.10, Fg 10.13
family treatment, 439
- Dentalium*, 431, 439, 443
Cretaceous, 99
- development, 436
external appearance, Fg 10.1
sensu stricto, 439
shell, Fg 10.1
Tertiary, 99
- Dentalium conspicuum*, 439
feeding, 434
spawning, 436
- Dentalium elephantinum*, 431, 439
as fossils, 437
- Dentalium (Fustiaria)*, 99
- Dentalium javanum*, shell, Fg 10.13
- Dentalium laqueatum*
larval shell, 436
- Dentalium sexangulum*
as fossils, 437
- Dentarene*, 673
- Denticelox*,
as fossil, 224
Ordovician, Tb 1.6
- Dentimargo*, 841
- Dentimitrella*, distribution, 829
- dentition, Bivalvia
see hinge dentition
- Dephinulidae, 674
- deposit-feeding, 42
Bivalvia, 206
Eucylcinae, 681
in mangroves, 45
Muricoidea, 820
Nuculoida, 206
Protobranchia, 209, 235
sandy sediments, 42
Sareptidae, 240
on shelf, 39
Solemyidae, 206
Tellinoidea, 209
Umboniinae, 689
- dermal cushions
Lepidoteuthidae, Fg 13.16, 526
- dermal structures
Lepidoteuthidae, Fg 13.16
- Dermatobranchus*, Pl 35, 938, 1007
- Dermatobranchus fortunatus*,
Fg 16.17, 1008
rhinophores, Fg 16.17
- Dermatobranchus pulcherrimus*,
941, 1008
- Dermatobranchus striatellus*,
Fg 16.19
egg masses, Fg 16.19
- Dermomurex*
calcified periostracum, 823
- Deroceras*
host of *Davainea proglottina*, 68
host of *Muellerius capillaris*, 68
- Deroceras laeve*
parthenogenesis, 19
- Deroceras panormitanum*,
external appearance, Fg 17.59
- Deroceras reticulatum*
alimentary tract, Fg 14.27,
Fg 17.7
external appearance, Fg 17.59
plant pest, 1103
reproductive system, Fg 17.59
- Deshayes, 337, 431
- desiccation
Hyriidae, 293
methods of reduction, 56
Pulmonata on land, 1045
- desiccation tolerance
Asaphis violascens, 346
- Desmoceras*, Cretaceous, 99
- desmodont system, Fg 4.6
- Desmophyllites*, Cretaceous, 99
- Desmopteridae, Fg 16.65, 980
characters, 47
family treatment, 985
- Desmopterus*, 985
- Desmopterus gardineri*, 985
- Desmopterus papilio*, Fg 16.65, 985
external appearance, Fg 16.65
- detorsion
Opisthobranchia, 565, 929
- detorsion, regulatory
prosobranchs, 614
- detoxification
Bivalvia, 211
Lucinidae, 313
- detritus-feeding
Cerithioidea, 708
Lepetidae, 649
Turritellidae, 708
- development, 320, 337, 363, 769, 853, 1063, 1068
Anomalodesmata, Fg 9.4, 216, 401
Architectonicoidea, 859
Basommatophora, 1050
Bivalvia, 195, 216
Caenogastropoda, 634, 703
Cephalopoda, 452, 469, 470
Cerithioidea, 708
Cirrata, 469
Cocculiniformia, 654
Coleoidea, 502
Corbiculoidea, 216
Cypraeoidea, 780
Dentaliida, 439
egg size, 634
Galeommatoidea, 216, 303
Gymnosomata, 986
Heterobranchia, 703
Heterodonta, 303
Mactroidea, 304
Muricoidea, 820
Neritoidea, 694
Opisthobranchia, 936
Palaeoheterodonta, 292
Patellogastropoda, 642
pelagic molluscs, 48
prosobranchs, 637
Protobranchia, 22
Pulmonata, 1051, 1055
Pyramidelloidea, 865
Rissooidea, 745
Scaphopoda, 436
Tellinoidea, 304, 342
Thecosomata, 980
Tonnoidea, 793
Tridacnoidea, 304
Trochoidea, 672
Unionoidea, 216
Valvatoidea, 856
- development, direct, 12
Bivalvia, 216, 217
Caenogastropoda, 638
effects on distribution, 58
Opisthobranchia, 590
- development, indirect
Gastropoda, 637
- development time
Gastropoda, 592
- Devonian, 95
Carditoidea, 322
marine transgressions, 90
Mecynodontidae, 348
molluscs, Fg 1.98
Nautilida, 491
nautiloid biogeography, 493
Neritoidea, 694
Neritopsina, 610
Oncocerida, 491
Orthocerida, 491
Scaphopoda, 437
- Diacavolinia*, 982
- Diacavolinia longirostris*, Fg 1.52,
Fg 16.62, 986
feeding web, Fg 1.50
shell, Fg 16.62
swarming, 49
- Diacria*, 923, 982
shell form, 923
- Diacria trispinosa*, Fg 16.62
shell, Fg 16.62
- Diadema*, as cassid prey, 583
- Diademoceras*, 491
- Diala*, 712, 714
distribution, 714
taxonomic placement, 714
- Diala albugo*, 714
protoconch, Fg 15.86
- Diala lirulata*, 714
radula, Fg 15.86
- Diala megapicalis*, 713, 714
protoconch, Fg 15.86, 712
- Diala semistriata*, 714
- Diala sulcifera*, 714
head-foot, Fg 15.86
- Diala suturalis*, 712–714
feeding, 713
operculum, Fg 15.86
pallial oviduct, Fg 15.86
shell, Fg 15.86
- Diala varia*, Fg 1.17
- Dialessa*, 714
- Dialia*, euspermatozoa, 714
- Dialidae, Fg 1.17, Fg 15.86, Tb 15.1
affinities, 712, 714, 718
characters, 712, 714
euspermatozoa, 708
family treatment, 712
- Dialopsis*, affinities, 714
- dialyneury, 628, 629
- Diaphana*, 932, 947, 948
- Diaphana brazieri*, Fg 16.26, 947
external appearance, Fg 16.26
shell, Fg 16.26
- Diaphana colei*, 947
- Diaphana minuta*, 947
- Diaphana tasmanica*, 948
- Diaphanidae, Fg 16.26
family treatment, 947
- Diaphanoidea, characters, 947
- Diaphorodoris*, 992
- Diaphoromactra*, 337
- Diaphoromactra versicolor*
distribution, 338
shell, Fg 8.22
- Diasoma*, 223, 438
component groups, 3
- Diastoma*, 730, 733
Miocene, 730
Oligocene, 730
Pleistocene, 730
Tertiary, 101
- Diastoma melanioides*, 729, 730
distribution, 729
ecology, 730
habitat, 729
operculum, Fg 15.95
protoconch, Fg 15.95
radula, Fg 15.95
shell, Fg 15.95
- Diastoma melanoides*
morphology, Fg 15.95
- Diastomatidae, Fg 15.95, Tb 15.1, 714, 729
affinities, 709, 730
family treatment, 729
as fossils, 714
taxonomy, 730
- Diastomidae, 730
- diaulism, Opisthobranchia, 932
- Dibaphimitra*, 842
- Dibranchia, 487
affinities, 485
- Dibranchiata, 452

- Dicathais*, 822
as fossils, 824
- Dicathais orbita*
distribution, 78, 823
external appearance, Fg 14.3
radula, Fg 15.157
shell, Fg 15.156
- Dicerocardiidae, 351
- Dicranodesma*, 320
- Dictyabyssia*, 662
- Dictyosphaeria*, 974
- Dicyathifer*
characters, 378
habitat, 374
- Dicyathifer manni*, 378
external appearance, Fg 8.52
habitat, 378
- diel activity cycle
Cephalopoda, 473
- Dieneroceras*, Triassic, 97
- Diffalaba*, 714
- digestion
Aplacophora, 147
Bivalvia, Fg 4.13, Fg 4.14, 16
Cephalopoda, 16, 457
Coleoidea, 500
enzymes, 15
Gastropoda, 14, 582, 586
Heterodonta, 302
Mollusca, 14
Myoidea, 364
Opisthobranchia, 918, 926
Polyplacophora, 14, 165
prosobranchs, 616
Protobranchia, 236
Pulmonata, 1042, 1043
Scaphopoda, 433
Stylommatophora, 1043
- digestion, external
Octopodidae, 549
- digestive cycles
Bivalvia, 209
Veneridae, 358
- digestive diverticula, Fg 4.13
Bivalvia, Fg 4.14, 209
- digestive duct appendages
Cephalopoda, 460
Coleoidea, Fg 11.14
Octopoda, 460
Sepioidea, 460
Teuthoidea, 460
- digestive enzymes
cephalopoda, 16
- digestive glands
Anomalodesmata, 399
Bivalvia, Fg 4.1
Calliostoma, 619
Cephalopoda, 460
Cocculiniformia, 654
Coleoidea, Fg 11.14, 500
Dentaliida, 434
functions, 586
Gadilida, 434
Gastropoda, 586
Myoidea, 364
Opisthobranchia, 918
Pulmonata, 1044
- digestive system, *Calliostoma*, 616
- digestive tubules
Bivalvia, Fg 4.14, 209
- Digidentis*, 941
- Dikoleps*, 691
- Diminovula*, 784
- Dimitobelus*
Cretaceous, 99
as fossils, 503
- Dimitobelus diptychus*
Cretaceous, Fg 1.100
- dimorphic spermatozoa
Epitoniidae, 816
- Galeommatidae, 316
- Muricoidea, 820
- dimorphism in shell
Cypracidae, 782
- Dimya corrugata*, 274
morphology, Fg 6.17
shell, Fg 6.17
- Dimyarina*, 274
- Dimyella*, 274
- Dimyidae, Fg 6.17
family treatment, 274
- Dimyioidea, description, 274
- Dinassovica*, 675
as fossils, 676
- Dinassovica jourdani*, 675
- Diniatys*, 954, 955
- Diodora*, 432, 669
Cretaceous, 99
excretory system, Fg 15.16
mantle cavity, Fg 14.15, Fg 14.16
sex change, 633
shell, 671
spawning, 631
- Diodora lineata*, shell, Fg 15.54
- Diodora nubecula*
spermatophore, 634
- Diodorini, 669
- Diodorinae, 669
- Diotocardia, 581
excretory system, Fg 15.16
heart, 16
- Diozoptysis*
as fossils, 735
- Diplodonta*, 310, 315
- Diplodonta globularis*
shell form, Fg 4.2, 199
- Diplodonta punctata*
ctenidial filament, section, Fg 8.6
- Diplodonta rotundata*, 315
- Diplodonta semiaspera*
morphology, Fg 8.6
- Diplodontidae, 315
- Diplommatina*
shell, 705
- Diplommatina (Eclogarinia)*, 706
- Diplommatina gowllandi*
distribution, 706
habitat, 706
shell, Fg 15.80
- Diplommatina sulcolliis*
radula, Fg 15.80
- Diplommatinidae, Fg 15.80,
Tb 1.5, Tb 15.1, 703
in Australia, 706
family treatment, 705
Lord Howe Island, 114, 706
Norfolk Island, 114, 706
- Diplommatininae, 705
- Diplomoceras*, Cretaceous, 99
- Diplomorpha*, 1096
- Dirocerithium*
as fossils, 735
- Dironidae, 1007
- Dischides*, 445
- discoblastula, Cephalopoda, 469
- Discoceras*, 491
- Discocharopa aperta*, 1099
distribution, 85
shell sculpture, Fg 17.3
- Discodorididae, 997
- Discodoris*, 919
- Discopoda, 703
- Discosorida, 487, 490
- Discosoroidea, 485
- Discotectonica*, 861, 862
- Discotectonica disca*, 861
- Discotectonica wannonensis*
Tertiary, Fg 1.101
- Discoteuthis*, 525
mantle, 525
- Discoteuthis discus*, 525
external appearance, Fg 13.15
- Discoteuthis laciniosa*
radula, Fg 13.15, 525
- discovery, HMS, 195
- Discrevinia*, 741
- Discrevinia balba*, 741
shell, Fg 15.101
- diseases
Cephalopoda, 471
Tridacnidae, 335
- dispersal
Achatinidae, 1089
Anomalodesmata, 402
anthropochorous bivalves, 222
Corbiculidae, 305
direct developers, 592
freshwater taxa, 84
larvae, 592
Nautilus, 495
non-marine Gastropoda, 592
Pandoridae, 416
Ranellidae, 800
Sphaeriidae, 62, 305, 355
Corixidae, 355
terrestrial molluscs, 58
Verticordiidae, 421
- dispersal mechanisms
Corbiculidae, 222
Hyriidae, 222
Sphaeriidae, 222
- dispyrene sperm
see paraspermatozoa
- Distorsio*, 799
diversity in Australia, 799
as fossils, 799
morphology, 799
proboscis, 793
shell, 798
- Distorsio anus*, 798
- Distorsio interposita*, 799
- Distorsio perdistora*
operculum, Fg 15.140
- Distorsio reticularis*
distribution, 798, 799
shell, Fg 15.140
- distribution, 351, 419, 495, 525,
545, 549, 704, 707, 747, 778,
1016, 1106, 1109
Acochlidia, 959
Anomalodesmata, 404
Australian marine division, 593
Australian pulmonates, 1057
Conoidea, 847
Corbiculoidea, 352
Cuspidarioidea, 404
deep water regions, 80
Dentaliida, 439
and earth history, 77
Endodontoidea, 1057
estuarine fauna, 79
freshwater molluscs, 82
Gymnosomata, 986
Heterodonta, 305
Hiattelloidea, 370
Histiotethidae, 530
Indo-West Pacific, 593
introduced molluscs, 80
marine, estuarine molluscs, 77
marine overlap zones, 78
marine provinces, 78
Neritoidea, 694
non-marine molluscs, 80
Orthurethra, 1080
overlap zones, 593
Palaeoheterodonta, 293
Papuinae, 1057
Parmacellidae, 1102
Patellogastropoda, 644
- Patelloidea, 645
pelagic molluscs, 80
plant limpets, 644
Poromyoidea, 404
Protobranchia, 236
Rissooidea, 746
and shipping activity, 940
terrestrial molluscs, 57, 85
Tridacnoidea, 332
tropical fauna, 593
tropical marine fauna, 79
Unionoidea, 293, 296
Unionoidea, 296
warm temperate fauna, 79, 593
- distribution patterns
Cardiidae, 223
Mytilidae, 223
- distributional changes
Aplacophora, 149
- ditaxy, 13
Pulmonata, 1041
- Ditremata, 1060
- Ditropis*
distribution, 704
habitat, 704
shell, 704
- Ditropis macleayi*, 704
- Ditropis whitei*, 704
- Divalucina*, 311
- Divalucina cumingi*, shell, Fg 8.3
- Divaricella quadrisulcata*
foot, Fg 8.3
- Divarilima*, distribution, 268
- diversity, 552, 1106, 1108
Acmaceoidea, in deep water, 648
Cancellarioidea, 846
Carinariioidea, 804
Cephalaspidea, 943
Cephalopoda, 451
Cerithioidea, 707
Chaetodermomorpha, 150
Coleoidea, 502
Dentaliida, 439
effects of salinity, 41
freshwater molluscs, 106, 107
Gastropoda, 565
Mactroidea, 337
Myoidea, 363
Nautiloidea, 452
Neomeniomorpha, 151
Neritoidea, 694
non-marine molluscs, 82, 106
Nudibranchia, 990
Palaeoheterodonta, 289
Patellogastropoda, 643
Patelloidea, 645
Pulmonata, 1052
Scaphopoda, 431
shelf molluscs, 39
Stylommatophora, 1062
terrestrial molluscs, 106
Thecosomata, 980
Thracioidea, 408
Trochoidea, 672
Unionoidea, 296
Unionoidea, 296
Veneroidea, 306
- diversity in Australasia
Orbitestellidae, 858
- diversity in Australia, 274
Amathinidae, 869
Amphibolidae, 1067
Amphitretidae, 546
Ancillinae, 835
Anomalodesmata, 404
Anomiinae, 281
Aplacophora, 145, 149
Architectonicidae, 861
Architeuthidae, 527
Arcidae, 254
Arcoidea, 254
Argonautidae, 552, 554
Athoracophoridae, 1109

- Bankiinae, 378
 Bathyteuthidae, 530
 Bolitaenidae, 546
 Brachioteuthidae, 532
 Bursidae, 794
 Camaenidae, 1056, 1112, 1113
 Cancellariidae, 846
 Cardidae, 330
 Carditidae, 324
 Carinariidae, 807
 Carinarioidea, 804
 Cassinae, 795
 Cerithiopsidae, 811
 Charopidae, 1056
 Chilodontini, 680
 Chiroteuthidae, 533
 Cingulopsidae, 743
 Clavagellidae, 414
 Clementiinae, 360
 Coleoidea, 499
 Columariinae, 825
 Columbelloidea, 827
 Condyllocardiidae, 325
 Conidae, 850, 852, 853
 Corbiculidae, 354
 Corbulidae, 366
 Coriillidae, 1110
 Costellariidae, 844
 Cranchiidae, 540
 Crassatellidae, 326
 Ctenopterygidae, 530
 Cucullaeidae, 254
 Cuspidariidae, 424, 425
 Cyamiidae, 320
 Cyclophoridae, 704
 Cycloteuthidae, 525
 Cymatiinae, 800
 Cypraeidae, 780
 Cystopeltidae, 1107
 Dentaliidae, 439
 Dosiniinae, 360
 Eatonellidae, 744
 Ellobiidae, 1078
 Enoploteuthidae, 521, 523
 Eulimidae, 817
 Fascioliariidae, 833
 Ficidae, 797
 Fimbridae, 313
 Galeommatidae, 318
 Gastrochaenidae, 368
 Glauconomidae, 362
 Glossidae, 352
 Grimalditeuthidae, 539
 Gryphaeidae, 270
 Haloceratidae, 772
 Harpidae, 838
 Helicarionidae, 1106
 Helicodiscidae, 1100
 Hemidonacidae, 332
 Hiatellidae, 370
 Hipponicidae, 771
 Histioeuthidae, 528, 530
 Hydrobiidae, 755
 Hyriidae, 289, 293, 298
 Idiosepiidae, 514
 Isognomonidae, 265
 Jouannetiinae, 376
 Joubiniteuthidae, 539
 Kelliellidae, 350
 Lamellarinae, 790
 Laternulidae, 404, 410
 Lepidoteuthidae, 526
 Limacidae, 1102
 Limidae, 268
 Limopsidae, 259
 Liotiinae, 673
 Littorinidae, 739
 Loliginidae, 517
 Lophinae, 272
 Lottiidae, 650
 Lucinidae, 311
 Lycoteuthidae, 520
 Mactridae, 338
 Mactromyidae, 315
 Marginellidae, 841
 Martesiinae, 375
 Mastigoteuthidae, 537
 Melongenidae, 832
 Mesodesmatidae, 340
 Myidae, 364
 Myochamidae, 404, 416
 Mytilidae, 250
 Nassariidae, 831
 Naticidae, 791
 Nautilidae, 495
 Neomeniomorpha, 151
 Noetiidae, 254, 258
 Nuculanidae, 239
 Nuculidae, 237
 Nudibranchia, 920
 Octopodidae, 549, 550
 Octopoteuthidae, 523
 Olividae, 837
 Omalogyridae, 864
 Ommastrephidae, 532, 533
 Onchidiidae, 1063
 Opisthobranchia, 941
 Opisthoteuthidae, 545
 Ostreinae, 271
 Ovulidae, 784
 Palaeoheterodonta, 289
 Pandoridae, 415
 Parilimyidae, 406
 Patellogastropoda, 640
 Pectinidae, 278
 Periplomatidae, 408, 409
 Petricolidae, 361
 Philobryidae, 260
 Pholadidae, 304
 Pholadinae, 375
 Pickworthiidae, 740
 Pinnidae, 265
 Pitarinae, 360
 Plicatulidae, 274
 Poromyidae, 423
 Pruvotinidae, 154
 Psammobiidae, 345, 346
 Pteriidae, 262
 Pulmonata, 1038, 1056
 Pulvinitidae, 265
 Rastodontidae, 744
 Rhytididae, 1091, 1093
 Rissoellidae, 864
 Samarangiinae, 360
 Sareptidae, 240
 Scaphopoda, 431, 432
 Semelidae, 344
 Sepiadariidae, 510
 Sepiidae, 508
 Sepiolidae, 511
 Sigmurethra, 1080
 Siliquariidae, 720
 Siphonariidae, 1068
 Solecurtidae, 346
 Solemyidae, 241
 Solenidae, 341
 Sphaeriidae, 355
 Spondyliidae, 279
 Sportellidae, 322
 Stenothyridae, 766
 Strombidae, 766
 Struthiolariidae, 768
 Subulinidae, 1088
 Succineidae, 1108
 Systellomatophora, 1062
 Tapetinae, 360
 Tellinidae, 343
 Terebridae, 851
 Teredinidae, 304, 376
 Teredininae, 378
 Testacellidae, 1108
 Thiaridae, 729
 Thraciidae, 404, 409
 Thracioidea, 408
 Thyasiridae, 314
 Thysanoteuthidae, 533
 Tonnidae, 802
 Tonnoidea, 792
 Trapeziidae, 349
 Tremoctopodidae, 552
 Trigonidae, 289, 295
 Triphoridae, 810, 811
 Triviinae, 787
 Trochidae, 680
 Trochinae, 683
 Trochoidea, 672
 Trochomorphidae, 1102, 1104
 Turridae, 848, 850
 Turritellidae, 718
 Ungulinidae, 315
 Unionoidea, 289
 Vampyromorphidae, 542
 Vasinidae, 825
 Veneridae, 357
 Veneroidea, 306
 Verticordiidae, 421
 Vitreledonellidae, 547
 Vitrinellidae, 764
 Volumitridae, 843
 Volutidae, 835
 Xenophoridae, 776
 Xylophaginae, 376
 Docoglossa, 606, 639
 docoglossate radula, Fg 1.14, 582, 619
 Dolabella, 976
 Dolabella auricularia, Fg 16.13, 936, 977
 gizzard, Fg 16.13
 Dolabellidae, 975
 Dolabra, Devonian, Tb 1.6
 Dolabrifera, 935, 976
 Dolabrifera dolabrifera, 977
 Dolabriferidae, 975
 Dolicholatirus, Cretaceous, 99
 Dolichonephra, 1060, 1080
 Dolicrossea labiata, 759
 Dolorthoceras, 491
 dolphin shells, 673, 674
 Domatoceras, 491
 Donacellidae, 339
 Donacidae, Fg 1.37, Fg 1.79, Fg 1.86, Fg 4.2, Fg 4.9, Fg 8.32, Pl 15, 76, 343
 catches, Fg 1.79
 characters, 346
 convergence with Mesodesmatidae, 347
 distribution of species, Fg 1.88
 family treatment, 346
 Donacilla
 on high-energy beaches, 37
 Donacilla angusta, 37
 Donaldinidae, Tb 15.1, 865
 Donax, 331
 burrowing, Fg 4.9
 ecology, 347
 movement and feeding, 302
 reproduction, 347
 Donax columbella, Fg 1.37
 distribution, 347
 Donax cuneata, distribution, 347
 Donax deltoidea, Pl 15, 340, 347, 348
 Aboriginal resources, 347
 age at sexual maturity, 347
 annual catches, Tb 1.3
 breeding season, 347
 catches, Fg 1.79
 development, 347
 distribution, 347, Fg 1.86
 fishery, 76, 221, 305
 on high-energy beaches, 37
 larval life, 347
 as prey, 37
 salinity tolerance, 347
 on sandy beaches, 37
 shell, Fg 8.32
 significance, 346
 size, 347
 spawning, 347
 Donax electilis, shell, Fg 4.2, 199
 Donax faba, distribution, 347
 Donax vittatus
 internal morphology, Fg 8.32
 Dondersiidae, Fg 2.3, Fg 2.7
 family treatment, 153
 Doratopsis larva, 533
 d'Orbigny, 452
 Doridella, Fg 16.71, Pl 35, 990-991
 external appearance, Fg 16.71
 Doridella obscura, 936
 development, 991
 Doridella steinbergae, 991
 effect on prey, 991
 Dorididae, Fg 16.11, Fg 16.15, Fg 16.16, Fg 16.82, Pl 35, 997
 family treatment, 998
 foregut, Fg 16.11
 jaw plates, Fg 16.11, Fg 16.82
 rhinophore, Fg 16.17
 in seagrass, 39
 Doridina, 990
 characters, 990
 diet, 938
 external appearance, Fg 16.2, 923
 internal morphology, Fg 16.3
 Nudibranchia, 990
 Doridoididae, 1008
 Doridomorpha, 1008
 Doridomorpha gardineri, Fg 16.96, 938, 1008
 external appearance, Fg 16.96
 feeding, Fg 16.96
 Doridomorphidae, Fg 16.96, 1007
 family treatment, 1008
 dorids, 923
 Doriopsis, 1000
 Doriopsis australiensis, 919
 Doris analampulla, 919
 Doris collatata, 919
 Doris maculosa, 919
 Doris pantherina
 painting, Fg 1.9
 Doris peculiaris, 919
 Doris praetenera, 919
 Doris pustulata, 919
 Doris pustulosa, 919
 dorsal bodies, Pulmonata, 1048
 Dorsaninae, 830
 dorso-ventral muscles
 Scaphopoda, 433
 Dorymenia, 155
 external features, Fg 2.12
 Dorymenia harpagata
 distribution, 155
 radular teeth, Fg 2.12
 Dorymenia sarsii
 radula and spicules, Fg 2.12
 Doryteuthis, 517
 shell, 517
 Doryteuthis bleekeri
 captive breeding, 519
 Dosidicus gigas, 532
 Dosina, Tertiary, 99
 Dosinia, 358, 360
 distribution of species, Fg 1.86
 habitat, 358
 Dosinia (Asa), 358
 Dosinia (Austrodosinia), 357, 358
 Dosinia caerulea, 359
 Dosinia (Dosinella), 358
 Dosinia (Dosinisca), 358
 Dosinia (Dosinobia)
 as fossils, 360
 Dosinia (Dosinorbis), 358



- Dosinia incisa*
biomass, 304
shell form, Fg 4.2, 199
- Dosinia juvenilis*, endemic, 357
- Dosinia (Keriaia)*, 358
- Dosinia (Pectunculus)*, 358
- Dosinia (Phacosoma)*, 358
- Dosinia victoriae*, sculpture, Fg 4.3
- Dosiniidae, 356
- Dosiniinae, 356, 358
- Dosinobia*, 360
- Dotidae, Fg 16.90, Pl 36
diet, 938
family treatment, 1004
- Doto*, Fg 16.2, 1004
external appearance, Fg 16.2
- Doto ostenta*, Fg 16.90, Pl 36
external appearance, Fg 16.90
radula, Fg 16.90
- doughboy scallop, Pl 5, Pl 13, 277
fishery, 73
- dove shells, 827
- Dreissena polymorpha*, 222
- Dreissenidae, 305
- Drilliinae, 850
- drilling
Dendrodoris citrina, 1000
Okadaia elegans, 996
- drought tolerance, 298
- Drupa*, 822, 823
diet, 823
diversity in Australia, 823
radula, 823
shell, 823
- Drupa grossularia*, shell, Fg 15.156
- Drupa ricina*, Fg 15.157
- Drupella*, 35
as coral predator, 35, 823
radula, 823
- Drupella cornus*,
on coral prey, Fg 1.29
- dugong
seagrass consumer, 38
- Dumont d'Urville, M.J., 196, 499,
568, 919
- Duperrey, Louis, 7
- Duplicaria*, 850
alimentary tract, 850
characters, 850
diversity, 851
habitat, 850
- Duplicaria duplicaria*
foregut, Fg 15.175
- Duplicaria evoluta*
shell, Fg 15.175
- Duplicaria ficitilis*, endemic, 851
- Durvillea antarctica*, 180
- Duyfken*, 6
- dwarf males
Argonautidae, 454, 552
Eulimidae, 817
Fossarinae, 722
Galeommatidae, 215, 303, 316
Galeommatidae, 215
Ocythoidae, 552
Teredinidae, 215
- dymantic displays
Galeommatidae, 220
Octopus, Fg 11.27
Sepia, Fg 11.27
Septoteuthis, Fg 11.27
- Dynamenella perforata*, 187
- Dynamenops diana*, 187
- Dysidea*, Pl 33, 953
and *Vulsella*, 263
- dysodont system, Fg 4.6
- dystenoid nervous system, Fg 15.17
- ear shells, 667
- earth history
and distributions, 77
- earthworms
as pulmonate prey, 15, 1107
- Eastonia*, 338
- Eatonellidae, characters, 743
- Eatonia ardea*, shell, Fg 15.102
- Eatonia condita*
operculum, Fg 15.102
radula, Fg 15.102
- Eatonia lunulata*
external appearance, Fg 15.102
- Eatonia micans*
anatomy, Fg 15.102
- Eatoniella*, 744
- Eatoniella depressa*
shell, Fg 15.103
- Eatoniella exigua*, shell, Fg 15.103
- Eatoniella fulva*, Fg 15.103
operculum, Fg 15.103
shell, Fg 15.103
- Eatoniella huttoni*
morphology, Fg 15.103
- Eatoniella olivacea*
morphology, Fg 14.1
- Eatoniellidae, Fg 15.103, Tb 15.1,
632, 741
buccal pouches, 621
family treatment, 743
- Eatonina*, 743
distribution, 743
subgenera, 743
- Eatonina fulgida*, 741
- Eatonina micans*, 741
- Eatonina sensu stricto*, 743
- Eatoniopsis*, 743
- Ebalidae, Tb 15.1, 865
- Ecculiomphalus*, Ordovician, 92
- Echineulima*
attachment to host, 817
diversity, 817
parasitism, 623
- Echineulima mittrei*
external appearance, Fg 15.154
snout, Fg 15.154
- Echinocephalus*
as pectinid parasites, 277
- Echinochama*, 309
- Miocene, 309
- Echinodermata
as bivalve predators, 219
as eulimid prey, 610
Eulimidae as parasites, 35, 817
as laterulid predators, 403
as ranellid prey, 799
as volutid prey, 833
- Echinogorgia*, as ovulid host, 786
- Echinoidea
as cassid prey, 796
as ranellid prey, 800
- Echinophoria*, 795
distribution, 796
as fossils, 797
- echinospira larva, 787
- Caenogastropoda, Fg 15.30
- Capulidae, 638, 774
- Capulus ungaricus*, 787
- Eratoidae, 638
- Lamellariidae, 638
- shell secretion, 787
- Triviidae, Fg 15.132
- Velutinidae, Fg 15.30, 790
- Velutinoidea, Fg 15.132, 786
- Echinostoma*, viviparid parasites,
707
- Echinostoma revolutum*, Tb 1.1
in humans, 69
- Echinostomatidae, Tb 1.1, 67
- Echinoteuthis*, 537
- Echiura, spiral cleavage, 22
- Eclipse*, 8
- ecological constraints
Heterodonta, 305
- ecological parameters
Teredinidae, 374
- ecological research
Patellogastropoda, 643
- ecological significance
Cephalopoda, 475
Corbulidae, 366
Heterodonta, 304, 305
Laternulidae, 412
Loliginidae, 519
Mactridae, 338
Mactroidea, 337
Muricoidea, 820
Tellinoidea, 342
- ecology
Anomalodesmata, 402
Cephalopoda, 471
Conidae, 853
Donacidae, 347
Heterodonta, 304
Littorinidae, 739
Mactridae, 338
Palaeoheterodonta, 293
Pulmonata, 1052
Scaphopoda, 437
Semelidae, 344
- economic significance
Bivalvia, 220
Cephalopoda, 475
Coleoidea, 502
Fasciola, 65
Heterodonta, 305
Limacidae, 1103
Lymnaeidae, 1071
molluscs as vectors, 65
Palaeoheterodonta, 293
paramphistomosis, 65
phylum Mollusca, 65
pollution, bivalve fisheries, 221
Polyplacophora, 175
Pulmonata, 1055
Scaphopoda, 437
schistosomes, 66
Siphiidae, 508
shipworms, 221, 305
Teredinidae, 221, 374
Unionoidea, 297
- Ecphorinae, 822
- ect-aquasperm
characteristics, 20
Patellogastropoda, 20
Vetigastropoda, 20
- ect-aquatic fertilisation, 634
- Ectenolites*, 493
- ectoparasites
Amathinidae, 868
Architectonicoidea, 859
Pyramidellidae, 865
- Ectorisma*, 422–424
- Ectorisma granulata*, 423
- Ectorisma neozelanica*, 424
- ectosiphuncle, Nautiloidea, 485
- Edentaria*, hinge, 424
- Edentellina*, 941, 965
- Edentellina typica*, 965
- Edmondia*
Permian, 97
Silurian, Tb 1.6
- Edmondiidae, 405
- egg capsules, 774, 867
Architectonicoidea, Fg 15.182,
859
Bivalvia, 216
Caenogastropoda, Fg 15.23,
Fg 15.27, 590, 636
Cerithioidea, 708
Conoidea, 847
Eulimoidea, Fg 15.154
freshwater taxa, 636
Gastropoda, Fg 14.33
Heterobranchia, Fg 15.182
Janthinoidea, Fg 15.151,
Fg 15.152
Littorinoidea, Fg 15.27,
Fg 15.605
Muricoidea, 820
Neogastropoda, Fg 15.166,
Fg 15.169
Neritopsina, Fg 15.73, 636
non-marine taxa, 637
Opisthobranchia, 935
pelagic, 590
production, 636
Rissooidea, 745
sand coating, Hydrobiidae, 755
Stromboidea, Fg 15.122
terrestrial taxa, 636
Teuthoidea, 469
Valvatoidea, 856
Vanikoroidea, Fg 15.123
Velutinoidea, 787
Vermetoidea, 778
- egg cases
elasmobranch, as food, 663
Naticoidea, Fg 15.135
Stromboidea, Fg 15.121
- egg collar, Naticoidea, 790
- egg cowry, Pl 26, 780
- egg formation, Pulmonata, 1050
- egg incubation, Cyamiidae, Fg 8.9
- egg laying, 24
Caenogastropoda, Fg 15.22,
Fg 15.24, Fg 15.26
Cephalopoda, 22, 51
Coleoidea, 501
Gastropoda, 590
pelagic molluscs, 48
Pulmonata, 1055
- egg masses, Fg 16.19, 713, 1063
Amphiboloidea, Fg 17.30
Anaspidea, 935
Architectonicoidea, Fg 15.183
Caenogastropoda, Fg 15.23, 635
Calliostoma, 631
Campaniloidea, Fg 15.98
Cephalaspidea, 936
Cephalopoda, 469
Cerithioidea, Fg 15.84, Fg 15.91
Coleoidea, 501
freshwater Pulmonata, 25
Gastropoda, Fg 1.20, 590
Gymnosomata, 986
Heterobranchia, Fg 15.183
marine Pulmonata, 25
Neomeniomorpha, 148
Neritopsina, Fg 15.26
Notaspidea, 936
Nudibranchia, 936
Oegopsida, 469
Opisthobranchia, Fg 16.19, 25,
590, 935
planktonic forms, 635
Polyplacophora, 173
prosobranchs, 632
Pulmonata, 590
Tonnoidea, Fg 15.143
types in Tonnoidea, 793
Vetigastropoda, Fg 15.21
- egg ribbons, 1068
Cerithiidae, 712
- egg shells
Pulmonata, 1038

INDEX

- egg size, 521
 Caenogastropoda, 634
 Patellogastropoda, 634
 prosobranchs, 634
 Vetigastropoda, 634
- egg strings
 Carinarioidae, Fg 15.147, 804
- eggs, 1091, 1106
 Anomalodesmata, 401
 Cephalopoda, 452
 numbers produced, 592
 Octopoda, 469
 Opisthobranchia, 934
 Scaphopoda, 436
 Sepioidea, 469, 501
 Stylommatophora, 1050
 Teuthoidea, 469
- Egilomen cochlidium*
 shell, Fg 17.55
- Elachisina*, 758, 759
 as fossils, 759
 shell, Fg 15.115
- Elachisina floridana*
 head-foot, 759
 reproduction, Fg 15.115
- Elachisina floridanus*, 758, 759
 habitat, 759
- Elachisina iredalei*, habitat, 759
- Elachisinidae*, Fg 15.115, Tb 15.1
 affinities, 758
 family treatment, 758
- Elachorhis*, 765
- Elachorhis tatei*, 764
- Elasmatinidae*, 1080
- Elasmias*, 1080, 1081
 shell, 1080
 viviparity, 1080
- Elasmias wakefieldiae*
 possible introduction, 1080
 shell and sculpture, Fg 17.40
- Electomacra*, 337
- Electra*
 as food of Corambidae, 991
- Electroma*, 262
 form, 261
 shell, 262
- Electroma georgiana*, Pl 10
 habitat, 262
- Electroma zebra*, habitat, 262
- Eledone*, 473
 arterial system, Fg 11.15
 sperm storage, 469
 venous system, Fg 11.16
- Eledone palari*, 549
 eggs, 549
 external appearance, Fg 13.35
 hectocotylus, Fg 13.35
- Eledonella*, 546
- Eledonella sheardi*
 distribution, 546
- Eledoninae*, 549
- elephant slug, 671
- Eleutheromenia*, 155
 abundance, 149, 154
 distribution, 155
 external appearance,
 Fg 2.1, Fg 2.11
- Eleutherorhabda*, 224
- Eliota*, 1009
- Ellatrivia*, Tertiary, 99
- Ellatrivia merces*, Pl 26
 shell, Fg 15.132
- Ellesmerocerida*, 485, 487, 489
- Ellobiidae*, Fg 1.47, Fg 1.48,
 Fg 14.6, Fg 14.27, Fg 17.19,
 Fg 17.37, Pl 31, 20, 1047,
 1067
 chiasoneury, 1047
 family treatment, 1076
- as fossils, 1057
 kidney, 1045
 phylogenetic significance, 589
 subfamilies, 1078
- Ellobiinae*, 1078
- Ellobioidea*
 description, 1076
- Ellobium*, 1078
 genital ducts, 1078
 habitat, 1078
 shell modification, Fg 14.6
- Ellobium aurisjudae*
 shell, Fg 17.37
- Ellobium aurismidae*
 shell, Fg 17.37
- Ellobium pellucens*,
 radula, Fg 17.37
 stomach, Fg 17.37
- Elminius*, 992
- Elsothera nautilodea*
 apical shell sculpture, Fg 17.55
- Elsothera* sp.
 external appearance, Fg 17.20
- Elysia*, Fg 16.2, Fg 16.48, 937,
 966, 967
 external appearance, Fg 16.2,
 Fg 16.48, 922
 and plastids, 940
- Elysia australis*, 919, 968
- Elysia bennetti*, 968
- Elysia cf. furvacauda*, 937
- Elysia chilensis*, 968
- Elysia coodgeensis*, 968
- Elysia filicauda*, 968
- Elysia furvacauda*, 968
- Elysia japonica*, 968
- Elysia leucolegnote*, 968
- Elysia maoria*, 934, 968
- Elysia ornata*, 968
- Elysia patina*, 968
- Elysiella*, 967
- Elysiella pusilla*, 968
- Elysiidae*, Fg 16.48
 family treatment, 967
- Elysioidea*, characters, 966
- Emarginula*, 669
 shell, 669
- Emarginulinae*, 669
- Emarginulini*, 669
- Emblanda*, 749
 feeding, 745
- Emblanda emblematica*
 feeding, 749
 head, Fg 15.107
 radula, Fg 15.107
 shell, Fg 15.107
- Emblandidae*, Fg 15.107, Tb 15.1,
 745
 family treatment, 749
 oviduct, 745
- Embletonia*, Fg 16.3, 1015
 internal anatomy, Fg 16.3
- Embletonia gracile*, Fg 16.106
 external appearance, Fg 16.106
 radula, Fg 16.106
- Embletonia pulchra*, 1015
- Embletoniidae*, Fg 16.106
 family treatment, 1015
- embryo retention, Gastropoda, 591
- embryogenesis, Pulmonata, 1051
- embryology
 Anomalodesmata, 401
 Aplacophora, 148
 Bivalvia, 216
 Cephalopoda, Fg 11.23,
 Fg 11.24, 469
 Coleoidea, Fg 11.23, Fg 11.24
 development time, 590
- Gastropoda, 591
- Heterodonta, 303
- Mollusca, 22
- Ommastrephidae, Fg 11.24
- Polyplacophora, 173
- Pulmonata, 1051
- Scaphopoda, 436
- Sepiidae, Fg 11.23
- Sepioidea, Fg 11.23
- Teuthoidea, Fg 11.24
- Emerita*
 as prey, 37
 on sandy beaches, 37
- Empleconia*, distribution, 259
- Endeavour*, 6, 10, 499, 521
- endemism, 1106
 Aplacophora, 149
 Architectonicidae, 862
 Arcidae, 256
 Australian pulmonates, 1057
 Batillariidae, 721
 Cancellariidae, 846
 Cardiidae, 223, 331
 Cleidothaeridae, 404
 Coleoidea, 502
 Columbidae, 829
 Conidae, 854
 Cystopeltidae, 1107
 Dialidae, 714
 Glycymerididae, 260
 Heterodonta, 305
 Hyriidae, 293
 Kimberley, 1057
 Littorinidae, 739
 Lottiinae, 651
 mytilid genera, 223
 Mytilidae, 223, 253
 non-marine mollusca, 80
 Notomenia, 149
 Octopodidae, 550
 Ommastrephidae, 533
 Opisthobranchia, 941
 Opisthoteuthidae, 546
 overlap zones, 593
 Ovulidae, 786
 Sepiadariidae, 510
 Sepiidae, 508, 509
 Sphaeriidae, 62
Splendrillia, 850
 Tellinoidea, 342
 transition zone bivalves, 222
 Trochidae, 680
 Turbininae, genera, 675
 Turridae, 848, 850
 Turritellidae, 718
 Umboniinae, 689
 Veneridae, 357
 Volutomitridae, 843
 warm temperate fauna, 593
- Endoceras*, Silurian, 95
- Endoceratidae*, 486
- Endoceratoidea*, 485
- Endocera*, 487, 489
 restoration, Fg 12.5
- endocone, Endocera, Fg 12.5
- endocytosis, Nuculidae, 239
- Endodontidae
 secondary ureter, 1046
- Endodontoidea, distribution, 1057
- endogenous sperm
 Opisthobranchia, 932
- endosiphuncle, Nautiloidea, 485
- endostyle, Caenogastropoda, 616
- endosymbionts, Lyonsiidae, 402
- Engina*, distribution, 827
- Engina armillata*
 operculum, Fg 15.159
 radula, Fg 15.159
 shell, Fg 15.159
- Enidae*, Fg 17.45, Tb 1.5, 85, 86
 family treatment, 1085
- lineages, 1086
 ureter, 1046
- Enigmonia*, 280, 281
 ciliary tracts, Fg 4.12
 distribution, 281
 eyes, 213
- Eninae*, lineages, 1086
- Ennucula*, Tb 1.6, 237
 Tertiary, 99
- Enoploteuthidae*, Fg 11.6,
 Fg 11.14, Fg 13.11,
 Fg 13.12, Pl 18
 family treatment, 521
- Enoploteuthinae*
 characters, 521
 depth range, 521
- Enoploteuthis galaxias*, Pl 18, 521
 distribution, 523
 external appearance, Fg 13.11
 hectocotylus, Fg 13.11
 radula, Fg 13.12
- Enotepteron*, 954
- Ensiculus*, 341
- Ensis*, 341
 burrowing, Fg 4.9
 distribution, 341
 fourth pallial aperture, 341, 398
 on sandy beaches, 37
 shell/body relationship, Fg 4.10
- Ensis arcuatus*
 internal morphology, Fg 8.26
- Ensis directus*, amino acids, 340
- Ensis siliqua*, sorting area, 341
- Ensisolen*, 341
- Entalimorpha*, 444
- Entalina*, 444
- Entalina mirifica*, 444
- Entalinidae*, Fg 10.19
 family treatment, 444
- Entalinopsis*, 444
- ent-aquatic fertilisation, 634
- Entemnotrochus*, 666
- Enteromorpha*, 955, 967, 975
- enteropneusts, as terebrid prey, 850
- enterotoxaemia
 economic importance, 68
- Enteroxenidae*, 817
- Entoconcha*, parasitism, 623
- Entoconchidae*, 817
- Entodesma*
 brooding, 401
 byssal gland, 399
 changes in oocyte, Fg 4.19
 development, 216
 mantle gland and secretion, 399
 sand bonding, 399
 shell microstructure, 398
- Entodesma cuneata*, 401
 eggs, 401
- Entoliidae*, 278
 extant species, 279
 family treatment, 279
- Entolium*, Tb 1.6, 279
 Cretaceous, 279
- Entovalva*, 318
 internal shell, 195
- enzymes
 amylase, 15, 364, 1043
 cathepsin B, 236
 cellulase, 364, 1044
 chitinase, 459, 1044
 coleoid digestion, 500
 digestive, 586
 glycogenase, 364
 proteases, 209, 400, 459, 1043
 sulphide oxidase, 243
 trypsin, 236

- Eocene, 752
Aturoidea brunnschweileri,
 Fg 12.10
 Campaniloidea, 733
Cellana, 647
Chama, 309
 Conoidea, 847
Diastoma, 730
Eutrophoceras geelongensis,
 Fg 12.10
 fossil record, 99
 Hiatelloidea, 370
Hipponix, 771
Kummelia, 368
 land snails, 1058
 Nautiloidea, 493
Nautilus, 495
 Oxynooidea, 962
 Pandoroidea, 415
Plicatula, 273
Sacoglossa, 961
Teichertia prora, Fg 12.10
 Tonnoidea, 794
 Trochoidea, 673
Eocithara
 as fossils, 838
Eocithara lamellifera
 as fossils, 838
Eocithera, Tertiary, 101
Eocylichna, 949
 Eogastropoda, Tb 14.1, Tb 15.1,
 609, 639
 features, 609
 status, 568
 Eolidae, in seagrass, 39
Eopteria, Ordovician, 93
Eopteria struszi
 Ordovician, Fg 1.98
Eoscapander, 949
Eoschizodus, Devonian, Tb 1.6
Eoschizodus taemasensis
 Devonian, Fg 1.98
Eotebenna, Cambrian, 89
Eotebenna pontifex
 Cambrian, Fg 1.97
Eothinoceras, 489
Eotrigonia, 294–296
 as fossil, 223, 293, 296
 Miocene, 294, 296
Eotrigonia eocenica
 fossil, Fg 7.7
Eotrigonia subundulata
 Tertiary, Fg 1.101
Eovolutilithes, Cretaceous, 99
Ephippodonta, 318
 dwarf males, 215
 shell, 318
Ephippodonta macdougalli, Pl 13
 hinge, Fg 8.8
 epiathroid nervous system,
 Fg 15.17, 628
 Heterobranchia, 628
 epibenthic sled, 40
 epibiota
Bivalvia, 224
 on mollusca, 44
Pyramidellidae, 44
Trigoniidae, 296
Epicodakia, 311
 epidermal glands
 Opisthobranchia, Fg 16.7
Epiglypta
 Lord Howe Island, 1106
Epiglypta howinsulae
 probable extinction, 114
Epigridae, Fg 15.109, Tb 15.1, 746
 family treatment, 751
Epigrus, 751
 distribution, 752
Epigrus cylindraceus, 751
 radula, Fg 15.109
 shell, Fg 15.109
Epimenia, 148, 156
 brooding, 148
 colour pattern, 146
 development, 148
 distribution, 149
 external features, Fg 2.13
 feeding, 156
 habitat, 156
 radular function, 147
 size at maturity, 156
 study animals, 145, 156
Epimenia arabica, 156
Epimenia australis, Fg 1.3, Pl 7,
 145, 148
 activity, 149
 captive care, 156
 depth range, 156
 diet, 156
 reproduction, 156
 righting behaviour, 151
Epimenia oshimai, 156
Epimenia verrucosa, 156
Epimeniidae, Fg 1.3, Fg 2.13, Pl 7
 family treatment, 156
 epiphragm
 Camaenidae, Fg 1.62, 1113
 Helicidae, 1113
 Helicodiscidae, 1100
 in land snails, 571
 Pulmonata, 1055
 Pupillidae, 1082
 Subulinidae, 1087
 terrestrial molluscs, 56
 epipodial lobes
 Dentaliida, 433
 Dentaliidae, Fgs 10.3–10.5
 epipodial sense organs, 630
 Pleurotomarioidea, 610
 Vetigastropoda, 629
 epipodial tentacles
 Choristellidae, 654
 Cocculiniformia, 654
 prosobranchs, 613
 Vetigastropoda, 629
 epipodium, prosobranchs, 613
 epiproboscis
 Mitridae, Fg 15.169, 841
 Mitrinae, Fg 15.169
 Neogastropoda, Fg 15.169
 epipsammic browsing
 Hydrobiidae, 620
Episiphon, Fg 10.17, 443
Episiphon bordaensis, 443
Episiphon tornatissimus, 444
Episiphon virgula, 443
 shell characters, Fg 10.17
 epistellar bodies, Octopoda, 467
Epitoniidae, Fg 14.4, Fg 15.152,
 Pl 24, Tb 15.1, 566
 association with prey, 816
 Australian genera/subgenera, 816
 as cnidarian predators, 813
 as coral predators, 34
 family treatment, 814
 locomotor wave form, 612
 Epitoniinae, 814
 Epitonioidae, 813
Epitonium, Pl 24, 34
 anemones as prey, 42
 distribution, 816
 jaws and feeding, 622
 salivary glands, 816
 sex reversal, 633
 shell, Fg 14.4, 814
Epitonium albidum, 816
 veliger, Fg 15.152
Epitonium clathrus
 extrovert, 815
 hermaphroditism, 633
Epitonium greenlandicum, 816
Epitonium imperialis
 external appearance, Fg 15.152
Epitonium jukesianum
 egg capsules, Fg 15.152, 816
 incubation period, 816
Epitonium millicostatum
 development, 816
 larval life span, 816
Epitonium scalare, Fg 15.152
Epitonium sensu lato, 816
Equichlamys bifrons, Pl 13, 275,
 277
 depth range, 277
 eggs, 277
 fishery, 73, 220, 277
 host to *Myochama*, 418
 nestling, 277
 pediveligers, 277
 shell, Fg 6.18
Erato, 632
 development, 787
 larval shell, 787
Erato voluta, 787
 Eratoidea, 774
 Eratoinae, 787
 diversity in Australia, 788
 eratos, 786, 787
Ercolania, 973, 974
Ercolania felinus, 973
Ercolania fuscata, 974
Ercolania margaritae, Fg 16.55,
 973, 974
 external appearance, Fg 16.55
Erdbachites, Carboniferous, 97
Eremopeas, distribution, 86
Eremopeas interioris
 distribution, 1088
 reproductive tract, Fg 17.47
 shell, Fg 17.47
Eremopeas tuckeri
 distribution, 1088
 shell, Fg 17.47
 Ergalataxinae, 822
Erichthonius, 514
Ericusa, as fossils, 835
Ericusa hamiltonensis
 Tertiary, Fg 1.101
 Eromanga Basin, Fg 1.95
Erosaria, 780
 Erosariinae, 780
Erronea, 780
 Erroneinae, 780
Ervilia, 344
 Ervilinae, 340
Erycinidae, 316
Erycinoidea, 316
 erythrocytes
 Aplacophora, 147
 Arcidae, 256
Epimenia, 147
 Phenacolepadidae, 700
Escalima, 268
 escape behaviour, 346
 Cardiidae, Fg 4.22
 Heterodonta, 305
 prosobranchs, 612
 Solenoidea, 340
 Umboniinae, 689
 Veneridae, 358
Estellacar, 257
Estellacar galactodes, 257, 258
 mantle cavity, 257
Estellacar olivacea
 distribution, 257
Estellacar saga, 257, 258
 estuaries
 ecosystem characteristics, 40
 habitat loss, 79
 molluscs, 40
 physical characteristics, 79
 estuarine molluscs
 distributions, 79
 economic importance, 41
 relationships, 79
 estuarine sediments
 intertidal sand beaches, 37
 subtidal sand plains, 37
 Etadunna Formation, 1058
Ethalia
 distribution, 689
 Etheridge, Robert Jnr, Fg 1.10, 10
 Etheriidae, 296
Ethminolia, distribution, 689, 690
Etrema curtisiana, shell, 848
Etrema obdita, Tertiary, Fg 1.101
 Euarminoidea
 characters, 1007
 rhinophore, Fg 16.17
Eubaculites, Cretaceous, 99
 Eubranchidae, Fg 16.102, Pl 36
 family treatment, 1012
Eubranchus inabai,
 Fg 16.102, Pl 36
 external appearance, Fg 16.102
Eubranchus sp., radula, Fg 16.102
Eucalyptus, 355, 1109
Eucharilda, 858, 859
Eucharilda elegantula, 859
Euchasma, Ordovician, 93
Euchelus, 680
 association, 672
 distribution, 682
 habitat, 680
Euchelus atratus, 681
 head-foot, Fg 15.61
 shell, Fg 15.61
Euchondria
 Carboniferous, 95
 Permian, 97
Euciroa, 401
Euciroa galathea, shell, Fg 9.16
Eucithara, shell, 848
Eucithara arenivaga
 acrosome, Fg 1.17
Eucithara coronata
 distribution, 848
 shell, Fg 15.174
Eucithara stromboides, radula, 849
 Eucla Basin, Fg 1.95, 1058
Eucleoteuthis, light organs, 532
Eucleoteuthis luminosa
 distribution, 533
Euconulus fulvus, 1105
Eucrassatella, 326
 Aboriginal resources, 326
 diversity, 326
 as fossils, 327
 as myochamid host, Fg 9.14
 pallial organs, 326
sensu stricto, 326
 size, 326
Eucrassatella cumingii, 402
 distribution, 326
 host to *Myochama*, 418
Eucrassatella decipiens
 internal morphology, Fg 8.14
 shell, Fg 8.14
Eucrassatella donacina
 distribution, 326
Eucrassatella kingicola
 distribution, 326
 host to *Myochama*, 418
Eucrassatella pulchra
 distribution, 326
 shell, Fg 8.14

INDEX

- Eucrassatella* (*Spissatella*)
as fossils, 326
- Eucrassatella verconis*
aboriginal resources, 305
- Euctenidiacea, 941
- Eucyclinae, 679, 682
description, 680
taxonomic history, 680
- Eudendrium*
as flabellinid prey, 1012
- Eudolium*, 793, 798, 802, 803
as fossils, 803
habitat, 803
as holothurian predator, 803
Tertiary, 101
- Eudolium bairdii*, 803
- Eudolium biornatum*, as fossils, 803
- Eudoridoidea, 990
characters, 997
diet, 938
external features, Fg 16.2
families, 997
Nudibranchia, 990
relationships, 997
rhizophore, Fg 16.17
as sponge predators, 997
- Eudoxochiton*, 181
- Eudoxochiton inornatus*, Pl 7, 173, 181
- Eufistulana*, 368, 370
boring, 368
burrow lining, 368, 369
distribution, 369
habitat, 363
mantle lobes, 368
shell, 368
siphons, 368
- Eufistulana australis*, 370
as fossils, 368
- Eufistulana mumia*
in burrow, Fg 8.43
morphology, 368
shell, Fg 8.43
- Eugabrielona sulcifera*
radula, Fg 15.58
- Eugaimardia*, 320
- eugarie, 347
- Euglandina*
biological control, 1090
- Euglandina rosea*, 109
adaptations to predation, 583
diet, 584
impact on indigenous molluscs, 58, 109
radular function, 583
- Eulima*, Pl 24, 817
diversity, 817
foot, 817
radula, 817
salivary gland, 817
sex reversal, 633
- Eulima acutissima*, shell, Fg 15.154
- Eulimella*
shell, 867
- Eulimidae, Fg 15.154, Pl 24, Tb 15.1, 817
attachment to host, 817
Australian genera, 817
as echinoderm parasites, 35, 817
family treatment, 817
hermaphroditism, 633
included taxa, 817
as parasites, 38, 623
prostate gland, 632
on sand plains, 38
- Eulimoidea, Tb 15.1, 703, 808
affinities, 808
characters, 817
description, 817
- Eulitoma*, diversity, 817
- Eumarcia*,
distribution, 360
habitat, 358, 360
- Eumetula*, habitat, 811
- Eumetulinae, 811
- Eunaticina*, 791
- Eunaticina papilla*, shell, Fg 15.134
- Euninella*, 675
- Euomphaloceras*, Cretaceous, 99
- Euomphaloidea, 856, 865
- Euomphalus*
Devonian, 95
Silurian, 95
- Euphausiidae
as carinariid prey, 806
- Euphemites*
Carboniferous, 95
Permian, 97
- Euphemites wynnensis*
Permian, Fg 1.99
- Euphuridae, 993
- Eupleura*, shell, 792
- Euplexaura*
as ovulid host, 786
prey of *Crenavolva tigris*, Pl 30
- Euprymna*, 511
luminescent organs, 511
- Euprymna berryi*, 514
- Euprymna cf. morsei*
arm crown, Fg 13.7
hectocotylus, Fg 13.7
- Euprymna hoylei*, 511
- Euprymna morsei*, 511, 514
behaviour, Fg 11.27
defence pose, Fg 11.27
external appearance, Fg 13.6
male tentacular club, Fg 13.7
mating behaviour, Pl 18
radula, Fg 13.7, 511
- Eupulmonata, 1037, 1047, 1067
description, 1076
- eupyrene sperm, 634
- see euspermatozoa, 20
- Eurhomalea*, 358
- Eurydesma*
Permian, 88, 97
- Eurydesma cordatum*
Permian, Fg 1.99
- Euselenops luniceps*, Fg 16.60, 979
external appearance, Fg 16.60
- Euselia*, distribution, 811
- euspermatozoa, Fg 1.17, 631, 634
Ampullarioidea, 20
Campaniloidea, 734
Cerithioidea, Fg 15.82, Fg 15.88, 707
Cerithioidea, 20
Cyclophoroidea, 20
modified, 20
Mollusca, 20
Nautiloidea, 20
Nudibranchia, Fg 1.17
Octopoda, 20
Patellogastropoda, 20
taxonomic value, 709
Trigonoidea, 20
Unionoidea, 20
Vetigastropoda, 20
- Eusphaeroma crenulatum*
as chiton symbiont, 175
- Euspira*, 791
Cretaceous, 99
- Euspira catena*
external appearance, Fg 15.134
mantle cavity, Fg 15.135
radula, Fg 15.135
- Euthecosomata
as atlantid prey, 804, 805
characters, 47, 980
external features, 923
- Euthriofusus*, Cretaceous, 99
- Euthyneura, 566, 568, 606, 854
status, 567
- euthyneury, 930
Gastropoda, 576
Opisthobranchia, 918
- Eutrechoceras*, 493
- Eutrechoceras geelongensis*, 492
- Evechinus*, as ranellid prey, 800
- evolution
Nuculoida, 224
post-Ordovician bivalves, 224
- evolutionary trends
Anomalodesmata, 404
Coleoidea, 451
Veneroidea, 307
- Excellichlamys spectabilis*
shell, Fg 6.18
- excretion
Anomalodesmata, 401
Aplacophora, 147
Bivalvia, 210
Cephalopoda, 463
Coleoidea, 463
Gastropoda, 581
Heterodonta, 303
Mollusca, 16
Octopoda, 463
Palaeoheterodonta, 291
Polyplacophora, Fg 3.11, 169
prosobranchs, 625
Pulmonata, 1045
Scaphopoda, Fg 10.9, 435
terrestrial Caenogastropoda, 627
terrestrial gastropods, Fg 1.64
- excretory system
Amimopina macleayi, Fg 17.12
Bivalvia, 211
Caenogastropoda, Fg 15.16
Calliostoma, 625
Coleoidea, Fg 11.17, 501
Nautiloidea, Fg 11.17
Neritidae, Fg 15.16
Neritopsina, Fg 15.16
octopus, Fg 11.17
Patellogastropoda, Fg 15.16, 642
Patelloidea, Fg 15.16
Pleurotomarioidea, Fg 15.16
prosobranchs, Fg 15.16, 625
Pulmonata, Fg 17.12
squid, Fg 11.17
Systellommatophora, 1045
Vetigastropoda, Fg 15.16
- excretory waste removal
Pulmonata, 581
- exhalant apertures
Tellinoidea, 302, 342
Tridacnoidea, 332
Unionoidea, 290
Veneroidea, 307
Veneroidea, 356
- exhalant siphon
Arcoidea, 204
Trigonoidea, 204
- Eximiothracia*, 408, 409
diversity, 409
- Eximiothracia modesta*, 409
- exogenous sperm
Opisthobranchia, 932
- exogenous sperm duct, Fg 16.18
- Exogyrinae, 269
- Exohaliotis*, 667
as fossils, 669
host to *Myochama*, 418
- Exosiperna*, endemism, 253
- Exosphaeroma*, 187
- experimental procedures
on rocky shores, 29
- exploitation
abalone, 669
current patterns, 36
Haliotidae, 669
Pinnidae, 267
Tridacnidae, 335
- external appearance, Fg 16.73, 525, 551, 552, 1100, 1105
Amphiboloidea, Fg 17.30
Anomalodesmata, Fg 9.5, Fg 9.9, Fg 9.11, Fg 9.14, 397
Aplacophora, 146
Architectonicioidea, Fg 15.182, Fg 15.183, 858
Arionoidea, Fg 17.58
Avacoidea, Fg 17.52
Basommatophora, Fg 17.31, 1041
Bivalvia, Fg 4.1, 196
Capuloidea, Fg 15.127
Cardioidea, Fg 8.16
Carinarioida, Fgs 15.145–15.147
Cephalaspidea, Fg 16.2, 922
Cephalopoda, Fg 11.1, Fg 11.2, Fg 11.9, Fg 11.10, Fg 11.27, Fg 12.1, Fgs 11.5–11.7, 453
Cerithioidea, Fg 15.87, Fg 15.91, Fg 15.92, Fg 15.97
Cingulopsoidea, Fg 15.102, Fg 15.104
Coleoidea, 453, 499
Conoidea, 846
Cyamioidea, Fgs 8.9–8.11
Cyclophoroidea, Fg 15.78
Cypraeoidea, Fg 15.130
Ellobioidea, 1076
Eulimoidea, Fg 15.154
Galeommatoidea, Fg 8.8
Gastrochaenoidea, Fg 8.43
Gastropoda, Fg 14.3, Fg 14.7, Fg 14.8
Glacidorboidea, 1075
Helicoidea, Fg 17.71
Heterobranchia, Fgs 15.179–15.187
Heterodonta, 301
Janthinoidea, Fg 15.152
Lepetelloidea, Fg 15.46
Limacoidea, Fgs 17.59–17.61, Fgs 17.63–17.65
Lymnaeoidea, Fg 17.34, Fg 17.35
Muricoidea, 820
Nacelloidea, 643
Naticoidea, Fg 15.134
Nautiloidea, Fg 11.1, Fg 11.10, Fg 12.1, 495
Neogastropoda, Fg 15.160, Fg 15.161, Fg 15.170, Fgs 15.165–15.167
Neritopsina, Fg 15.75
Notaspidea, Fg 16.2
Octopoda, Fg 11.1, Fgs 13.35–13.38
Olividae, Fg 15.165, 835
Omalogyridae, Fg 15.185, 864
Ommastrephidae, Fg 11.6, Fg 11.10, Fg 13.22, 532
Onchidiidae, Fg 17.26, 1063
Opisthobranchia, 922
Otinoidea, 1062
Palaeoheterodonta, 289
Partuloidea, Fg 17.45
Patellogastropoda, 643
Patelloidea, 643
Pholadoidea, Fg 8.45, Fg 8.52, Fgs 8.47–8.50
Polyplacophora, 163
Ptenoglossa, Fg 15.149, Fg 15.150
Pulmonata, Fg 17.1, Fg 17.21, 1039
Pyramidelloidea, Fg 15.186, Fg 15.187, 865



- Rathousioidea, Fg 17.27,
Fg 17.28, 1064
Rhytidoidea, Fg 17.51
Rissoelloidea, Fg 15.184, 862
Rissooidea, Fg 15.113,
Fgs 15.116–15.120, 745
Sacoglossa, Fg 16.2, 922
Scaphopoda, Fg 10.1, Fg 10.5
semi-slug, Fg 17.1
Sepioidea, Fg 11.1, Fg 11.5,
Fg 13.1, Fg 13.2, Fg 13.4,
Fgs 13.6–13.8
slug, Fg 17.1
snail, Fg 17.1
Solenioidea, Fg 8.26
Stromboidea, Fg 15.21
Succinoidea, Fg 17.67
Systellommatophora, 1041,
Fg 17.58
Tellinoidea, Fg 8.27, Fg 8.29,
Fg 8.31
Teuthoidea, Fg 11.1, Fg 11.2,
Fg 11.6, Fg 11.9, Fg 11.10,
Fgs 13.9–13.11,
Fgs 13.13–13.28
Tonnoidea, Fgs 15.136–15.138,
Fg 15.142, Fg 15.144, 793
Triphoroidea, Fg 15.149,
Fg 15.150
Valvatoidea, Fgs 15.179–15.181
Vampyromorpha, Fg 11.10
external ligament
Parilimyidae, 406
extinction
conservation, 107
Lord Howe Island, 114
molluscan classes, 5
Norfolk Island, 114
Notopala hanleyi, 65
Notopala sublineata, 65
Phillip Island, 114
Placostylus cuniculinus, 114
Posticobia norfolkensis, 114
extinction rates, 106
extracellular digestion, 14
Gastropoda, 586
Scaphopoda, 434
extrapallial cavity, Bivalvia, Fg 4.8
extrapigmentary ocellus, Fg 3.20
Polyplacophora, 171
extravittelline food
Volutidae, 835
extrovert
Epitoniidae, Fg 15.152
Janthinidae, Fg 15.151
Janthinoidea, Fg 15.151,
Fg 15.152
eye morphology
Limacidae, Fg 17.15
Octopodidae, Fg 11.20
eyes, 499
Anomalodesmata, 401
Anomioidea, 280
Architectonicoidea, 859
Arcoida, 213
Basommatophora, 1041
Bivalvia, 18, 212, 213
Caenogastropoda, Fg 15.19
Cardioidea, 212
Cephalopoda, 453
Coleoidea, 467
Myopsida, 517
Oegopsida, 520
Opisthobranchia, 932
Patellogastropoda, Fg 15.19
Pectinoidea, 213
prosobranchs, Fg 15.19, 629
Pteriomorpha, 212
Pulmonata, Fg 17.15, 1041, 1048
Stylommatophora, 1079
Systellommatophora, 1041
Vetigastropoda, Fg 15.19
Eyre Peninsula Basin, Fg 1.95, 42
Eyrena, Cretaceous, Tb 1.6
Facelina, 1013
Facelininae, Fg 16.104, Fg 16.105
faeces
Cystopeltidae, Fg 17.64
prosobranchs, 621
Fairbankia, 752
Falcidens, 151
depth range, 149
distributional changes, 149
Falcidens lipuros, Fg 2.5
depth range, 151
external features, Fg 2.5
Falcidens poias, depth range, 151
Falciferella, Cretaceous, 99
Fallartemis, 360
false ears, 684
false jingle shells, 416
false limpets, 669
fan shells, 265
Fanulena, Norfolk Island, 1106
Fasciola, 67
economic importance, 65
Fasciola gigantica, 70
parasite, *Lymnaea auricularia*, 70
Fasciola hepatica, Fg 1.75, 64, 66,
67, 69, 1071
life cycle, 66
vectors, 1056
Fasciolaria
mating behaviour, Fg 14.29
Fasciolariidae, Fg 1.14, Fg 15.163,
Pl 28, Tb 15.1, 827
characters, 833
familial limits, 820
family treatment, 832
predation, 699
on reef slope, 35
Fasciolariinae, 833
characters, 833
Fasciolidae, 66
fasciolosis
economic significance, 66
in humans, 69
Pseudosuccinea columella, 67
Fastigiella, 712
Fastosarion, distribution, 1106
Fastosarion aquila
external appearance, Fg 14.7,
Fg 17.1, Fg 17.63
faunal affinities
deep-sea molluscs, 40
faunal decline
Murray River gastropods, 62
faunal regions
marine coastal, Fg 1.87
non-marine molluscs, 81
terrestrial, Fg 1.90
Faunus, 708
Fautor, in Australia, 686
Favorininae, Fg 16.104, Fg 16.105,
1013
Favorinus, 938, 974, 1013
feeding, 1011
Favorinus japonicus, Fg 16.19,
Fg 16.105
egg masses, Fg 16.19
radula, Fg 16.105
Fax, 827
fecundity
Achatinidae, 1089
Architeuthidae, 528
Argonautidae, 554
Bivalvia, 216
Coleoidea, 469
Enoplateuthidae, 521
Epitoniidae, 816
Hyriidae, 298
Octopodidae, 549
Octopoteuthidae, 523
Ocythoidea, 552
Opisthobranchia, 934
Pectinidae, 277
Tremoctopodidae, 551
Tridacnidae, 335
Xylophaginae, 218
Fedikovella, 656
feeding
Aeolidina, 1011
Anadoridoidea, 990
ancestral gastropod, 585, 605
Anomalodesmata, 399, 400
Aplacophora, 147
Architectonicoidea, 858
Bivalvia, Fg 4.12, 16
Cardioidea, 322
Carinariaidea, 804
Cephalaspidea, 937
Cephalopoda, 457, 459
Cerithioidea, Fg 15.89, 707
ciliary-feeding, 15
Coleoidea, 471, 500, 502
conversion efficiency, 508
Corbiculoidea, 352
Dendronotina, 1002
Dentaliida, 434
Elysioidea, 966
Eulimoidea, 584, 610
Gadilida, 434
Galeommatoida, 207
Gastropoda, 14, 582
Gymnosomata, 926, 986
Heterodonta, 209, 302
Janthinoidea, Fg 15.151, 610
Limapontioidea, 969
Mactroidea, 337
Melibe leonina, 584
Mollusca, 14
Muricoidea, 820
Myoida, 362
Myoidea, 364
Neogastropoda, 819
Neomeniomorpha, 149, 151
Neritoidea, 694
ontogenetic change, Coleoidea,
471
Opisthobranchia, Fg 16.12, 926,
937
Oxynooidea, 962
Palaeoheterodonta, 290
Polyplacophora, 14, 165
prosobranchs, 616
protobranch ancestor, 235
Protobranchia, 209, 235
Pulmonata, 1042
pulmonate buccal function,
Fg 17.9
pulmonates on land, 1052
Pyramidelloidea, 865
Rhytidoidea, 1091
Rissooidea, 745
Scaphopoda, Fg 10.1, 16, 433,
434, 437
septibranch bivalves, 16
shipworms, 302
Solenioidea, 340
Tellinoidea, 342
Thecosomata, 926, 980
Tonnoidea, Fg 15.137,
Fg 15.138, Fg 15.142,
Fg 15.144
Triphoroidea, 610
Valvatoidea, 854, 856
Velutinoidea, 786
Veneroidea, 355
without a radula, 584
feeding behaviour
Muricidae, 823
Pyramidellidae, 867
feeding chamber
Sareptidae, Fg 5.7, 240
feeding cycle, Veneridae, 358
feeding morphology
Amathinidae, Fg 15.187
Heterobranchia, Fg 15.186,
Fg 15.187
Pyramidellidae, Fg 15.186
Pyramidelloidea, Fg 15.186,
Fg 15.187
feeding tube, Lucinidae, Fg 8.3
Fermepalaina, 706
Ferreiraella, 175, 178
Ferrissia, 63, 1071, 1072
abundance in Murray River, 62
association with *Vallisneria*, 63
distribution, 84
form groups, 63
shell form, 63
Ferrissia neozelanica, 1072
Ferrissia petterdi, 63, 1071
distribution, 1072
external appearance, 1072
form group, 63
septation, 1072
shell, Fg 17.32
Ferrissia sensu lato, 63
Ferrissia tasmanica, 63, 1071,
1072
apical sculpture, Fg 17.32
external appearance, 1072
form group, 63
radula, Fg 17.32
reproductive anatomy, Fg 17.32
shell, Fg 17.32
Ferrissidae, 1072
Ferrussacia folliculus, 1087
distribution, 1087
shell, Fg 17.46
Ferrussaciidae, Fg 17.46
derivation of name, 1087
family treatment, 1087
fertilisation, 12, 24
Bivalvia, 216
Cephalopoda, 469
Cocculiniformia, 654
ect-aquatic, 634
ent-aquatic, 634
external, prosobranchs, 631
Gastropoda, 590
Heterodonta, 303
internal, prosobranchs, 631
Pulmonata, 1050, 1051
Scaphopoda, 436
stacking in limpets, 642
Tridacnoidea, 332
Unionoidea, 292
fertilisation chamber, Fg 16.18
fertilisation pocket
Pulmonata, 1048
fertilisation strategies, 24
Ferrussaciidae, Tb 1.5
fibrillar structure, Fg 15.32
Fibroceras, 490
Ficidae, Fg 15.138, Tb 15.1, 792
family treatment, 797
Ficus, 793, 794, 797–799, 803
burrowing, 797
distribution, 798
feeding, Fg 15.138
as fossils, 798
proboscis, 793
Ficus altispira, as fossils, 798
Ficus eospila,
external appearance, Fg 15.138
Ficus reticulata, radula, Fg 15.138
Ficus subintermedia, 797
sexual dimorphism, 797
shell, Fg 15.138

INDEX

- Ficus tessellata*
distribution, 798
protoconch, 798
- Fidera*, Ordovician, 92
- fig shells, 797
- filaments, 542
Vampyroteuthidae, 542
- Filaroides osleri*, in dogs, 68
- file shells, Pl 11, 267
- Filibranchia, 225
- filter-feeding,
Cerithioidea, 708
Heterodonta, 301, 305
Palaeoheterodonta, 290
Siliquariidae, 707, 708
Tridacnidae, 302, 333
Turritellidae, 707, 708
Umboniinae, 689
- filtrate composition
bivalve kidney, 211
- filtration, prosobranchs, 627
- filtration rates, 343
Bivalvia, 211
Unionoidea, 291
- Fimbria*, 310, 313, 314
- Fimbria fimbriata*, 313
distribution, 313
internal morphology, Fg 8.4
shell, Fg 8.4
- Fimbria sowerbyi*, 313
shell, Fg 8.4
- Fimbriatella maoria*, 859
- Fimbriidae, Fg 8.4, 309, 1005
family treatment, 313
- fin
Coleoidea, 500
function in Cephalopoda, 457
Octopoda, 545
Teuthoidea, 515
- fin, accessory, 538
- fin shape
Teuthoidea, Fg 11.10
Nautilidae, Fg 11.10
- Finella*, 732, 733
euspermatozoa, 708
external appearance, 732
- Finella fabrica*, 733
- Finella pupoides*
external appearance, Fg 15.97
operculum, Fg 15.97
protoconch, Fg 15.97
radula, Fg 15.97
shell, Fg 15.97
- Finellidae, 732, 733
- fingernail shells, 340, 352
- Fiona*, 938, 1017
janthinids, siphonophores, 814
- Fiona pinnata*, Fg 1.49, 1017
external appearance, Fg 16.108
feeding, 1011
radula, Fg 16.108
- Fionidae, Fg 1.49, Fg 923
family treatment, 1017
in plankton, 47
- Firoloida*, 807
egg string, 804, 808
- Firoloida desmaresti*, 807
distribution, 804, 808
egg strings, 49
external appearance, Fg 15.147
radula, Fg 15.147
swarming, 49
trematode parasite, 808
- fish bones as food, 663
- fish parasites, Marginellidae, 839
- fisheries, 72
abalone, 73
Amusium balloti, 220
Amusium pleuronectes, 220
Anadara, 256
Anadara trapezia, 221, 256
Arcidae, 76, 256
bivalves in Australia, 220
blue mussels, 76
Cellana, 647
cephalopod catch, global, 476
cephalopods, 74, 475, 499
clams, 220
Coleoidea, 502
Concholepas peruviana, 823
cowries, 783
Crassostrea gigas, 220
Cypraeacassis rufa, 794
Donax, 76
Donax deltoidea, 221, 305, 347
Equichlamys bifrons, 220
Katelsysia, 221
Lambis lambis, 768
Loliginidae, 502, 519
molluscs, 72
Muricoidea, 820
mussels, 220
Mytilus, 253
Mytilus edulis planulatus, 220, 221
Nototodarus gouldi, 533
Octopodidae, 74, 502, 550
Ommastrephidae, 74, 476, 502, 533
Ostrea angasi, 220, 271
Ostreidae, 74
oysters, 220
Panopea generosa, 371
pearl shell and pearling, 72, 221, 262
Pecten fumatus, 220
Pectinidae, 277
Pinctada albina, 221
Pinctada maxima, 221
pipis, 221
Placunidae, 282
pollution and bivalves, 221
Saccostrea amasa, 220
Saccostrea commercialis, 220
Saccostrea echinata, 220
scallops, 73, 220
Sepiidae, 502, 508
Solenidae, for bait, 341
squid jigging, 502
Strombidae, 768
Strombus gigas, 768
Strombus luhuanus, 768
Tridacnidae, 305, 335
trochus, 75, 683
Trochus niloticus, 672
Turbinidae, 76
Turbo marmoratus, 676
Turbo undulatus, 676
Veneridae, 76
- fishes
as molluscan predators, 43, 219, 437, 511, 519, 804, 853
as conid prey, 853
- fishing methods, Cephalopoda, 476
- Fissidentalium*, 439
external appearance, Fg 10.5
- Fissidentalium megathyris*, morphology, Fg 10.4
- Fissidentalium yokoyamai*
shell, Fg 10.14
- Fissilabia*, 722, 724
distribution, 724
- Fissilabia decollata*, 724
- Fissilabia decollata*
embryonic shell, Fg 14.36
- Fissilunula*, Tb 1.6, 348
Cretaceous, 348
- Fissilunula clarkei*, Tb 1.6
- Fissipulsellum*, 444
- Fissurella
boring by *Hiatella*, 371
- Fissurellidae, Fg 1.14, Fg 1.23, Fg 14.15, Fg 14.16, Fg 15.16, Fg 15.54, Pl 22, Tb 15.1, 29, 669
in Australia, 669
ctenidia, 578
exhalant opening, 18
family treatment, 669
kidney function, 625
pallial organs, 615
papillary sac, 626
podocytes, 627
subradular organ, 630
- Fissurellidini, 669
- Fissurellinae, 669
- Fissurelloidea, Tb 15.1, 664
description, 669
features, 610
- Fitzroy, Lieutenant Robert, 7
- fixation techniques, 102
- Flabellina*, 1012
- Flabellina ornata*, Fg 1.9
- Flabellina rubrolineata*, Fg 16.101
external appearance, Fg 16.101
radula, Fg 16.101
- Flabellinidae, Fg 16.101, Pl 37
family treatment, 1011
- flagship species, 106
- flamboyant display
Octopodidae, Fg 11.27
- Flammulinidae, 86
- Flemingites*, Triassic, 97
- Fletcheri*, Devonian, 95
- flexoglossate radula, 619
Orthogastropoda, 652
- Flinders, Lieutenant Matthew, 7
- Flinders Ranges, Fg 1.95
- Flindersian Province, 78
Cerithiopsidae, 811
- Florimetis obesa*, palps, 343
- Floripatella*, Palaeozoic, 645
- flotation
Janthinidae, Fg 15.151, 813
Janthinoidea, Fg 15.151
- Fluctiger*, 327
- Fluctiger royanus*, 327
- fluid-feeding
Gastropoda, 583
Pyramidellidae, 865
- Fluvidona*, 63, 83
distribution, 755
generic group of hydrobiids, 63
- fluvifaunal provinces, Fg 1.89
- fluvifaunulae, concept validity, 81
- Fluviolanatus*, 348–350
endemic, 349
musculature, 205
- Fluviolanatus subtorata*
ctenidia, Fg 4.12
distribution, 350
habitat, 350
shell, Fg 8.33
- Fluviopupa*, 63
distribution, 755
- Fly HMS*, 7, 196, 919
- Foliaeiscala*, in Australia, 816
- foliated calcite layer, Fg 4.7
- Fonscochlea*, 63, 83
radiation, 64
- Fonscochlea zeidleri*, Fg 1.70
- food eggs, Fg 15.23
see nurse cells, 24
- food sorting
Bivalvia, 208
Calliostoma, 618
- food sources
intertidal sand beaches, 37
- food string in Gastropoda, 585
- foot
Achatinoidea, 1087
Anomalodesmata, 399
Anomioidea, 280
Aplacophora, 145
Arcoidea, 253
Bivalvia, Fg 4.1
burrowing in Bivalvia, 13
Carditoidea, 322
Corbiculoidea, 352
Dentaliida, 439
evolutionary importance, Bivalvia, 223
extension in Bivalvia, 205
functions in Gastropoda, 574
Galeommatoidea, 316
glandular secretion, 612
Heterodonta, 302
Limacoidea, 1102
Limopsoidea, 258
locomotion, 13, 611
Lucinoidea, 309
Mactroidea, 336
Muricoidea, 820
musculature, 611
Myoidea, 363
Neomeniomorpha, 145, 146
Opisthobranchia, 925
Ostreina, 268
Otinoidea, 1062
Pandoroidea, 415
Pholadoidea, 372
Polygyroidea, 1110
Pteriomorpha, 249
Pulmonata, 1041
Pyramidelloidea, 865
Rhytidoidea, 1091
Scaphopoda, 433
sigmurethran groups, 1086
Solemyoidea, 241
Solenioidea, 340
Thracioidea, 407
Valvatoidea, 855
Veneroidea, 356
- Foramellina*, 265
- Foramellina exempla*, 265
endemic, 265
shell, Fg 6.11
- Foraminifera
as cephalopods, 452
as ovulid prey, 836
- Fordilla*, 223
as fossil, 223
as a pteriomorph, 223
shell features, 223
shell ultrastructure, 223
- foregut
Pupa kirki, Fg 16.11
Rostanga arbutus, Fg 16.11
- form, evolution
Bivalvia, Fg 4.5
- form groups, Ancyliidae, 63
- Fossacallista*, 360
- Fossaridae, 722, 769, 772
- Fossarinae, 722
characters, 722
- Fossarus*, 722, 724
brooding, 722
cerithioidean features, 722
protoconch, 722
radula, 722
- Fossarus ambiguus*, 722, 724
brood pouch, Fg 15.91
- fossil faunas, Bivalvia, Tb 1.6
- fossil record
Acanthochitonidae, 188
Acavoidea, Tb 17.3
Achatinellidae, Tb 17.3, 1081
Achatinelloidea, Tb 17.3
Achatinoidea, Tb 17.3
Acteonidae, 944
Amathinidae, 869

- Angariinae, 675
 Anomalodesmata, 404
 Anomioidea, 280
 Architectonicidae, 861, 862
 Arcidae, 256
 Arcticoidea, 348
 Arionoidea, Tb 17.3
 Assimineidae, 757
 Astartidae, 328
 Athoracophoridae, Tb 17.3
 Atlantidae, 806
 Barleeidae, 747
 Basommatophora, 1057, 1067
 Batillariidae, 722
 Belemnidae, 503
 Bithyniidae, 761
 Bivalvia, 223
 Buccinidae, 827
 Bulimulidae, Tb 17.3
 Bulimuloidea, Tb 17.3
 Bullidae, 958
 Caecidae, 763
 Caenogastropoda, 594
 Cainozoic, 99
 Calliostomatinae, 686
 Calyptracidae, 774
 Camaenidae, Tb 17.3, 1058, 1113
 Camaenoidea, Tb 17.3, 1112
 Cambrian, Fg 1.97
 Cancellariidae, 846
 Capulidae, 774, 775
 Carboniferous, Fg 1.99
 Cardioidea, 328
 Carditidae, 322
 Carinariidae, 807
 Caryodidae, Fg 17.24, Tb 17.3, 1058
 Cassidae, 795, 797
 Cephalopoda, 451
 Cerithiidae, 712
 Cerithiopsidae, 811
 Chamidae, 307
 Charopidae, Tb 17.3
 Cingulopsidae, 741
 Clavagellidae, 415
 Cleidothaeridae, 420
 Cocculinidae, 656
 Cocculiniformia, 654
 Coleoidea, 503
 Columbariinae, 825
 Condylacardiidae, 324
 Conoidea, 847
 Corbiculoidea, 353
 Corbulidae, 366
 Costellariidae, 845
 Crassatellidae, 327
 Crassatelloidea, 325
 Crassostreinae, 273
 Cretaceous, Fg 1.100
 Cryptoplacidae, 189
 Cucullaeidae, 257
 Cuspidariidae, 425
 Cuspidarioidea, 424
 Cyamiidae, 320
 Cyamioidea, 318
 Cylichnidae, 949
 Cylleninae, 830
 Cymatiinae, 800
 Cypraeidae, 784
 Cypraeidae, 784
 Cystopeltidae, Tb 17.3
 Dentaliida, 437
 Devonian, Fg 1.98
 Dialidae, 714
 Diaphanidae, 947
 Diastomatidae, 730
 Dimyidae, 274
 Dorsaninae, 830
 Eatonellidae, 744
 Elachisinidae, 759
 Ellobiidae, 1057
 Enidae, Tb 17.3, 1086
 Epigridae, 752
 Epitoniidae, 816
 Eucyclinae, 682
 Eulimidae, 817
 Eupulmonata, Tb 17.3, 1076
 Fasciolaridae, 833
 Ficidae, 798
 Fissurellidae, 671
 Gabrieloninae, 677
 Gadilidae, 437
 Galeommatidae, 318
 Gastrochaenidae, 370
 Gastropoda, 594
 Glacidorbidae, 1075
 Glossidae, 351, 352
 Glycymerididae, 260
 Haliotidae, 665, 669
 Halistylinae, 689
 Haminoidea, 955
 Harpidae, 838
 Helicarionidae, Tb 17.3
 Helicinidae, 702
 Helicodiscidae, Tb 17.3
 Hemidonacidae, 332
 Heterodonta, 301, 306
 Hiattelloidea, 363, 370
 Hipponicidae, 771
 Hydrobiidae, 755
 Hydrocenidae, 701
 Hydrococcidae, 763
 Hyriidae, 294, 298
 Iravadiidae, 752
 Isognomonidae, 265
 Janthinidae, 814
 Juliidae, 964, 965
 Kelliellidae, 350
 Laevidentaliidae, 437
 Laternulidae, 412
 Limacoidea, Tb 17.3, 1102
 Limoida, 267
 Limopsidae, 259
 Liotiinae, 674
 Littorinidae, 739
 Lophinae, 272
 Lord Howe Island, 1058
 Lottiinae, 650
 Lymnaeidae, 1057
 Mactridae, 339
 Malleidae, 264
 Marginellidae, 841
 Megaspiridae, Tb 17.3, 1089
 Melongenidae, 832
 Mesodesmatidae, 340
 Mesozoic, 97
 Mitridae, 842
 Muricidae, 824
 Muricoidea, 820
 Myochamidae, 419
 Nassariidae, 831
 Naticidae, 792
 Nautiloidea, 489
 Neoleptonidae, 321
 Nepean Island, 1058
 Neritidae, 700
 Neritimorpha, 693
 Neritoidea, 694
 Neritopsidae, 695
 Noetiidae, 258
 Norfolk Island, 1058
 Nuculanidae, 240
 Nuculidae, 239
 Omalogyridae, 865
 Ommastrephidae, 533
 Onychoteuthidae, 525
 Opisthobranchia, 594
 Orbitestellidae, 858
 Ordovician, Fg 1.98
 Orthurethra, Tb 17.3, 1080
 Ostreidae, 270
 Ostreinae, 271
 Ostreoida, 269
 Ovulidae, 786
 Palaeoheterodonta, Fg 7.7, 294
 Palaeozoic, 89
 Pandoridae, 416
 Pandoroidea, 415
 Partuloidea, Tb 17.3
 Patellidae, 647
 Patellogastropoda, 644
 Patelloidinae, 652
 Pectinidae, 278
 Periplomatidae, 410
 Permian, Fg 1.99
 Personidae, 799
 Pharidae, 341
 Phenacolepadidae, 700
 Philinidae, 951
 Philobryidae, 261
 Physidae, 1057
 Pinnidae, 267
 Pisanianuridae, 799
 Placunanomiinae, 281
 Placunidae, 282
 Planaxidae, 724
 Planorbidae, 1057, 1058, 1074
 Pleurotomariidae, 666
 Pleurotomarioidea, 665
 Polyplacophora, 176
 Pomatiopsidae, 756
 Potamididae, 727
 Propeamussiidae, 278
 Ptenoglossa, 808
 Pteriidae, 262
 Pterioidea, 261
 Pulmonata, Fg 17.24, Tb 17.3, 594, 1057
 Pulvinitidae, 265
 Punctidae, Tb 17.3
 Pupillidae, Tb 17.3
 Pupilloidea, Tb 17.3, 1082
 Pyramidellidae, 867
 Pyramidelloidea, 865
 Ranellinae, 800
 Retusidae, 950
 Rhytididae, Tb 17.3
 Rhytidoidea, Tb 17.3, 1091
 Ringiculidae, 946
 Rissoidae, 751
 Rissoida, 746
 Sacoglossa, 961
 Scaphopoda, 437
 Scissurellidae, 665, 667
 Seguenziidae, 693
 Septidae, 503
 Sigmurethra, Tb 17.3, 1086
 Siliquariidae, 720
 Siphonodentaliidae, 437
 Skeneidae, 691
 Solariellinae, 688
 Solemyidae, 244
 Solemyoidea, 241
 Solenidae, 341
 Spirulirostridae, 503
 Spondyliidae, 279
 Sportellidae, 322
 Stenothyridae, 766
 Strombidae, 768
 Stylommatophora, Tb 17.3, 1057
 Subulinidae, Tb 17.3
 Succineidae, Tb 17.3, 1109
 Succineoidea, Tb 17.3
 Tellinoidea, 343
 Terebridae, 851
 Tertiary, Fg 1.101
 Thecosomata, 980
 Thiariidae, 728
 Thraciidae, 409
 Tonnidae, 803
 Tonnoidea, 793
 Trapeziidae, 348
 Triassic, Fg 1.100
 Tricoliinae, 678
 Tridacnidae, 336
 Tridacnoidea, 332
 Trigoniidae, Fg 7.7, 293, 294
 Triphoridae, 811
 Triviidae, 788
 Trochidae, 680
 Trochoidea, 673
 Trochomorphidae, Tb 17.3
 Truncatellidae, 758
 Tudiclinae, 825
 Turbinidae, 673
 Turbininae, 676
 Turridae, 850
 Turritellidae, 718
 Umboniinae, 690
 Valvatoidea, 856
 Vanikoridae, 772
 Veneridae, Tb 8.2, 360
 Vermetidae, 780
 Verticordiidae, 422
 Vesicomidae, 351
 Vetigastropoda, 594
 Vitrinellidae, 765
 Viviparidae, 707
 Volutidae, 835
 Volutomitridae, 843
 Xenophoridae, 778
 Zonitidae, 1102
 Fothergill, Dr John, 6
 fourth pallial aperture
 Anomalodesmata, 398
 Cleidothaeridae, 419
 function, 398
 Mactroidea, 398
 Myochamidae, 418
 Pandoroidea, 415
 Parilimyidae, 406
 Periplomatidae, Fg 9.9, 410
 Pharidae, Fg 8.26
 Thraciidae, 408
 Verticordiidae, 420
 Verticordioidea, 420
Fractarmilla, 683
Fragum, 331, 336
 beach, 330
 building blocks, Fg 8.16
 Cardiidae, 328
Fragum erugatum
 density, 330
 distribution, 331
 in hypersaline waters, 41
 superabundance, Fg 1.41
Fragum fragum
 in middens, Fg 1.36
 symbiotic algae, 332
 use in jewellery, 330
Fragum hemicardium
 shell form, Fg 4.2
Fragum retusum, shell, Fg 8.15
Fragum unedo
 Aboriginal resources, 330
 external appearance, Fg 8.16
 in middens, 72
 shell, Fg 8.15
 symbiotic algae, 332
Fremblya, 184, 185
Frenamya, 415, 416
 freshwater Bivalvia, 196
 freshwater molluscs
 adaptations, 606
 Australian families, Tb 1.4
 conservation, 107
 distribution and affinities, 82
 Neritidae, 695
 origins, 606
 speciation, 746
 freshwater mussels, 59
 Hyriidae, 297
Friginatica, 791
Friginatica beddomei
 shell, Fg 15.134
 frog shells, 794
 frontal/vertical lobe system
 Coleoidea, 466
 Férussac, 1038
Fryeria, 924, 1000, 1001
 Fucales, substrata for limpets, 644
Fulvia, 328, 331
 hinge plate, Fg 4.6
Fulvia tenuicostata
 distribution, 331
 shell, Fg 8.15
 fungi and pulmonates, 1054
 funnel, Cephalopoda, 453
 Nautilidae, Fg 12.11, 485
 Taoniinae, 540

INDEX

- funnel cartilages
Cephalopoda, Fg 11.3, 453
Sepioidea, 504
Spirulidae, 504
Teuthoidea, 515
- funnel fusion, Cranchiinae, 540
- funnel groove
Illicinae, Fg 13.22
Ommastrephinae, Fg 13.22
Todarodinae, Fg 13.22
- funnel locking apparatus, 545
Architeuthidae, 527
Argonautidae, 552
Bathyteuthidae, 530
Brachyteuthidae, 532
Chiroteuthidae, Fg 13.24, 533
Ctenopterygidae, 530
Cycloteuthidae, 525
Enoplateuthidae, 521
Grimalditeuthidae, 538
Histiotteuthidae, 528
Idiosepiidae, 514
Joubiniteuthidae, 539
Lepidoteuthidae, 526
Loliginidae, 517
Lycoteuthidae, 520
Mastigoteuthidae, Fg 13.25, 537
Myopsida, 517
Octopoteuthidae, 523
Ocythoidae, 552
Oegopsida, 520
Ommastrephidae, Fg 13.22, 532
Onychoteuthidae, 523
Sepiariidae, Fg 13.5, 509
Sepioidea, Fg 13.5
Sepiolidae, 511
Teuthoidea, Fgs 13.22–13.24, 515
Thysanoteuthidae, Fg 13.23, 533
- funnel retractor muscles
Cephalopoda, Fg 11.3
- funnel structure
Cephalopoda, Fg 11.3
- Fusarium* spp.
transmission by molluscs, 72
- Fusculima*, diversity, 817
- Fusiaphera*, distribution, 846
- Fusiniinae, 833
characters, 833
- Fusinus*
carnivory, 42
Cretaceous, 99
- Fusinus australasia*, 277
- Fusinus novaehollandiae*
operculum, Fg 15.163
shell, Fg 15.163
- Fusitriton magellanicus*
distribution, 801
veliger, 802
- Fustiaria*, 439
- Fustiaria caesura*, 442
shell, Fg 10.15
- Fustiaria stenochizum*, 442
- Fustiariidae, family treatment, 439
- G**
- Gabbia*
distribution, 761
diversity, 761
as fossils, 761
habitat, 760
as host to *Clonorchis sinensis*, 760
- Gabbia australis*, Tb 1.1, 70, 761
distribution, 63, 83
external appearance, Fg 15.116
habitat, 63
head, Fg 15.116
operculum, Fg 15.116
- radula, Fg 15.116
resistance to desiccation, 63
shell, Fg 15.116
- Gabriel, Charles John, 11, 163, 568, 569, 1039
- Gabrielona*, 677, 678
- Gabrielona neapeanensis*, 677
distribution, 677
shell, 677
- Gabrielona pisinna*, 677
operculum, Fg 15.58
shell, Fg 15.58, 677
- Gabrieloninae
in Australia, 673, 677
description, 676
- Gadila*, 431, 437, 445
as fossils, 437
- Gadila acuminatus*, 446
- Gadila gaultina*, 437
as fossils, 437
- Gadila mucronatus*, 446
- Gadila spretus*, 446
shell features, 447
- Gadilida, 431
description, 443
- Gadilidae, Pl 16
family treatment, 445
as fossils, 437
- Gadilimorpha, description, 444
- Gadilina*, 443
- Gadilina tatei*, 444
- Gadilina triquetum*, 444
- Gadilinae, 445
- Gadiliniidae, family treatment, 443
- Gafrariinae, 356, 358
- Gafrarium*, 358, 360
habitat, 358
shell, 358
- Gafrarium tumidum*, 359
- Gaimard, Joseph P., 162, 196, 289, 499, 919, 1038
- Gaimardia*, 319, 320
- Gaimardia finlayi*, 320
internal morphology, Fg 8.9
- Gaimardia (Neogaimardia)*, 320
- Gaimardia tasmanica*
shell and hinge, Fg 8.9
- Gaimardian fluvifauna
freshwater molluscs, 81
- Gaimardian Province, Fg 1.89
- Gaimardiidae, 318
- Galadistes*, habitat, 1052
- Galathea*, 236
- galaxiids, as hyriid hosts, 293
- Galaxura*, 410
- Galeodea*, 794, 795, 798
- Galeodea maccamleyi*, 794
jaw, Fg 15.137
operculum, 795
radula, Fg 15.137
- Galeojanolus*, 1009
- Galeolaria*, 671, 1063
as prey of *Pseudoskenella*, 867
- Galeolaria caespitosa*, 32
- Galeomma*, 318
external appearance, Fg 8.8
- Galeomma polita*
dymantic display, 220
- Galeomma takii*, 318
defensive chemicals, 220
- Galeommatidae, Fg 4.12, Fg 4.22, Fg 8.8, Pl 13
family treatment, 316
- Galeommatoida
description, 316
families, 316
and Holothuria, 219
- Galeroconcha
see Monoplacophora, 3
- Galilee Basin, Fg 1.95
- galloping, 1042
- Galtoceras*, 491
- gamete production, 23
- gametoduct, Aplacophora, 147, 148
- gametogenesis
Cucumerunio novaehollandiae, 292
timing in bivalves, 24
- gametolytic sac, Fg 16.18
- Gammarus*, 502
- Ganatidae, Fg 16.42
family treatment, 960
- Ganesa*, radula, Fg 15.70
- Gangetia*, 766
- ganglia
Gastropoda, 576
- ganglion morphology
Pulmonata, 1048
- ganglionic fusion, 628
Opisthobranchia, 930
- Ganitus*, 960
- gape, Bivalvia, 198
- Gari*, 345
escape response, 346
habitat, 345
shell, 345
- Gari crassula*, habitat, 345
- Gari kenyoniana*, distribution, 346
- Gari lessoni*, shell, Fg 8.30
- Gari tellinella*, 345
- Garidae, 345
- garlic snail, 1104
- gas exchange
Bivalvia, 211
prosobranchs, 624
Scaphopoda, 434
terrestrial taxa, 625
Tridacnidae, 333
- Gascoignella*, 969
- Gascoignella aprica*, Fg 16.50, 969
external appearance, Fg 16.50
- Gascoignellidae, Fg 16.50
family treatment, 969
- gastric shield, Fg 15.11
- Buccinidae, 621
- Calliostoma*, 618
- Chaetodermatidae, 151
- Heterodonta, 302
- Ungulinidae, Fg 8.6
- Gastrochaena*, 367–370
boring, 368
burrow lining, 368
distribution, 369
sensu stricto, 369
siphons, 368
- Gastrochaena (Cucurbitula)*, 369
shell boring, 369
- Gastrochaena cuneiformis*
in burrow, Fg 8.43
morphology, 368
shell, Fg 8.43
- Gastrochaena cymbium*
in burrow, Fg 8.43
morphology, 368
shell, Fg 8.43
- Gastrochaena dubia*, 369
- Gastrochaena frondosa*
distribution, 368
- Gastrochaena gigantea*, Pl 16, 368
in burrow, Fg 8.43
shell, Fg 8.43
- Gastrochaena tasmanica*
distribution, 368, 369
shell boring, 369
- Gastrochaena (?) terra-reginae*
as fossils, 368
- Gastrochaenidae, Fg 8.43, Pl 16
as borers, 44
family treatment, 367
genera, 368
on reef slope, 35
- Gastrochaenoidea, 226
affinities, 370
description, 367
- Gastrocopta*, 86, 1084
shell, 1082
- Gastrocopta hedleyi*, Fg 17.42
- Gastrocopta macrodon*, 85
- Gastrocopta margaretae*
external appearance, Fg 14.4
- Gastrocopta pediculus ovatula*
radula, Fg 17.42
- Gastrocopta recondita*
distribution, 85
- Gastrocoptinae
genera, 1084
- Gastrodeuteia, Fg 4.13
- Gastropempta, Fg 4.13
- Gastropoda
amateurs and curators, 568
as bivalve predators, 219
bivalved taxa, 922
Cambrian, Fg 1.97
as cancellariid prey, 846
Carboniferous, Fg 1.99, 95
carnivory, 15
characters, 3, 565
checklists and monographs, 569
as conid prey, 853
Cretaceous, Fg 1.100, 99
definition and description, 565
Devonian, Fg 1.98, 95
digestion, 14
as fascioliid prey, 833
feeding, 14
in freshwater, 580
general features, 12
higher classification, 568
on land, 580
marine taxa, 569
inland waters, 62
musculature and locomotion, 573
nervous system, 576
non-marine taxa, 569
Ordovician, Fg 1.98, 92
parasitism, 15
Permian, Fg 1.99, 97
phylogeny, Fg 15.1, Fg 15.2, 606
protoconch, 13
radiation, 605
radula structure, Fg 1.14
recent classification, 567
sense organs, 18, 576
shell muscle, 13
Tertiary, 100
torsion and asymmetry, 565
traditional classification, 567
without shells, 573
- Gastropoteia, Fg 4.13
- Gastropteridae, Fg 16.4, Fg 16.9, Fg 16.10, Fg 16.32, Pl 33
evolution of body form, Fg 16.4
evolution of shell, Fg 16.4
family treatment, 952
- Gastropteron*, 954, 974
- Gastropteron bicomutum*, Fg 16.10, 918
external appearance, Fg 16.4
radular teeth, Fg 16.10
shell, Fg 16.4
- Gastropteron pacificum*, 954
- Gastropteron rubrum*, 954
- Gastropteron vespertilium*, 953
- Gastrotetartika, Fg 4.13
- Gastrotiteia, Fg 4.13

- gastrula, Cuspidariidae, 425
- gastrulation
- Anomalodesmata, 401
 - Aplacophora, 148
 - Bivalvia, 216
 - Pulmonata, 1051
 - Scaphopoda, 436
- Gatliff, John Henry, 11, 163, 196, 568, 569
- Gatliffena*
- distribution, 829
 - shell, 827
- Gaudryceras*, Cretaceous, 99
- Gaza superba*
- head-foot, Fg 15.62
 - radula, Fg 15.62
 - shell, Fg 15.62
- Gazameda*, 718
- Gazameda gunni*, 716
- Gazelle*, 145
- Geelwink*, 6
- Gegania valkyrie*, 859
- circulation, 859
 - egg mass, Fg 15.182, 860
 - head-foot, Fg 15.182
 - operculum, Fg 15.182
 - radula, Fg 15.182
 - reproduction, Fg 15.182
 - shell, Fg 15.182
- Geisonocera*, 491
- Geitodorididae, 997
- Geloina*, 354
- Gemellima*, 268
- Gemma*, 360
- brooding, 356
- Gemmidae, 356
- Gemminae, 356, 360
- distribution, 360
- Gemmula deshayesii*
- radula, Fg 15.175
- Gena*, 684
- habitat, 680
 - shell, 685
- Gena incola*, 685
- Gena strigosa*
- external appearance, Fg 14.7
- gene flow in direct developers, 592
- genetic differentiation
- Hydrobiidae, 755
- genetic studies, conservation, 107
- genital ducts
- Hydrobiidae, Fg 15.22
 - Neritidae, Fg 15.22
 - Neritopsina, Fg 15.22
 - Rissoidea, Fg 15.22
 - Stenoglossa, Fg 15.22
 - Triviidae, Fg 15.22
- genital pore, Pulmonata, 1041
- genitalia, Pulmonata, 1050
- Genota nicklesi*, radula, 849
- geoduck, 370
- exploitation, 371
- Geomelania*, 758
- habitat, 758
- Georgina Basin, Fg 1.95, 88
- Georissa*
- in Australia, 701
 - distribution, 85
- Georissa laseroni*
- distribution, 701
 - operculum, Fg 15.76
 - radula, Fg 15.76
- Georissa minuta*
- distribution, 701
- Georissa multilirata*
- distribution, 701
- Georissa obesa*, distribution, 701
- Georissa postulata*
- distribution, 701
- Gergovia*, distribution, 846
- Germon germon*, 552
- Gerridae, Fg 1.53
- Geukensia*, 203
- Giant African Snail
- external appearance, Fg 17.21
- giant clams, Pl 14, 332
- economic importance, 75
 - hatcheries, 75
 - mariculture, Fg 1.83, 75
 - see also Tridacnidae
- giant nerve fibres
- Cephalopoda, 18
 - Coleoidea, 466
 - Loliginidae, 517
 - Ommastrephidae, 533
- Gibberula*, 841
- Gibbula*, 680
- reproductive system, Fg 14.28
- Gibbula cineraria*
- respiration, 625
- Gibbula tumida*
- spawning, 631
- Gibbula umbilicalis*
- sensory papillae, Fg 15.20
- Gibbulinae, 679, 683
- Gibbulini, 683
- gill arrangement
- Polyplacophora, Fg 3.2, Fg 3.13
- gill filaments, Bivalvia, Fg 4.12
- gill homology
- Opisthobranchia, 929
- gill leaflets, 663
- Choristellidae, 664
 - Cocculinellidae, 663
 - Lepetellidae, 661
 - Osteopeltidae, 663
 - Phyllidiidae, 1001
- gill structure
- Opisthobranchia, 929
 - Polyplacophora, Fg 3.14
- gills
- Aplacophora, 146
 - Basommatophora, 1067
 - Chaetodermomorpha, 146
 - Cocculiniformia, 654
 - Cocculinoidea, 654, 655
 - dendritic, 923
 - eulamellibranch, 18
 - filibranch, 18
 - functions, 11, 18
 - general features, 11
 - Lepetelloidea, 654, 658
 - Opisthobranchia, 579
 - Patellologastropoda, 640
 - Polyplacophora, 168
 - prosobranchs, 578
 - pseudolamellibranch, 18
 - structure in Bivalvia, 18
 - see also ctenidia
- gills, secondary
- Chromodorididae, Fg 1.15
- Gippsland Basin, Fg 1.95
- Giraliapecten*
- Cretaceous, Tb 1.6, 99
- Girtyoceras*, Carboniferous, 97
- Girtypecten*, Permian, 97
- gizzard
- Anaspidea, 926
 - Anomalodesmata, 209
 - Aplysiidae, 976
 - Bullactidae, 955
 - Bulloidea, 957
 - Cephalaspidea, 926
 - Cylichnidae, 948
 - Cymbuliidae, 984
 - Haminoidea, 926, 955
 - Limacinidae, 981
 - Opisthobranchia, Fg 16.13, Fg 16.14
 - Peraclididae, 983
 - Philinidae, 950
 - Philinoidea, Fg 16.14
 - Retusidae, 950
- gizzard plates
- Cylichnidae, Fg 16.14
 - Opisthobranchia, Fg 16.13, Fg 16.14
 - Philinidae, Fg 16.14
 - Philinoidea, Fg 16.14
 - Retusidae, 950
- glaciations and distribution, 77
- Glacidorbidae, Fg 17.36, Tb 1.4
- family treatment, 1075
 - in freshwater, 62
 - in inland waters, 63
 - operculum, 1039
 - taxonomic history, 854
 - taxonomic status, 107
- Glacidorbiformes, 854
- Glacidorbiidae, 1067
- Glacidorbis*, 25, 1075
- affinities, 1075
 - distribution and habitat, 63, 84
 - diversity, 84
 - Gondwanan origins, 62
 - Miocene fossil, 84
 - operculate pulmonate, 63
 - taxonomy, 1075
 - viviparity, 1075
- Glacidorbis hedleyi*, 1075
- egg mass, 25
 - radula, Fg 17.36
 - reproduction, Fg 17.36
 - shell, Fg 17.36
- Glacidorbis magellanicus*, 1075
- Glacidorbis occidentalis*, 1075
- Glacidorbis paupela*
- brooding, 25, 1075
- Glacidorbis pedderi*, 1075
- Glacidorboidea, description, 1075
- Glacipisum*, 355
- gladius
- Coleoidea, 500
 - Cycloteuthidae, 525
 - Loliginidae, 517
 - Octopoda, 545
 - Octopoteuthidae, 525
 - Sepioidea, 453
 - Sepiolidae, 510, 511
 - Teuthoidea, 453, 515
 - Vampyromorpha, 542
- gland of Leiblein, 585
- Columbellidae, 829
 - Costellariidae, 843, 844
 - derivation, 621
 - Marginellidae, Fg 15.168, 839
 - Melongenidae, 831
 - Muricidae, 822
 - Muricoidea, Fg 15.155, 610
 - Neogastropoda, Fg 15.155, Fg 15.164, Fg 15.168, 622, 819, 822
 - Scaphellinae, Fg 15.164
 - Turbinellidae, 825
 - Volutidae, Fg 15.164, 835
 - Volutomitridae, 842
- Glans*, 324
- Glans ? hirasei*, distribution, 324
- glass snails, 1104
- Glaucidae, Fg 1.49, Pl 4, Pl 36
- egg mass, Fg 16.19
 - external appearance, Fg 16.104
 - Facelininae, Fg 16.19, Fg 16.104, Fg 16.105, 1015
 - family treatment, 1013
 - Favorininae, Fg 16.104, Fg 16.105, 1013
 - Glaucinae, Fg 16.104, 1015
 - Hervellinae, 1015
 - nematocysts and defence, 48
 - in neuston, 594
 - in plankton, 47
 - Pteraeolidinae, Fg 16.104, Fg 16.105, 1015
 - relationships, 1013
- Glaucilla*, Fg 1.49, 936, 1015
- Glaucilla marginata*, 926
- Glaucomyidae, 362
- Glaucome*, 362
- Glaucome cerea*
- distribution, 362
- Glaucome plankta*
- distribution, 362
- Glaucome rugosa*, 362
- distribution, 362
 - size, 362
- Glaucome virens*, 362
- distribution, 362
 - size, 362
- Glaucomeidae, 362
- Glaucomididae, Fg 8.40, 356, 362
- family treatment, 362
 - and Psammobiidae, 345
- Glaucus*, 936, 938, 1015
- egg laying, 49
 - janthinids, siphonophores, 814
 - and *Physalia* nematocysts, 925
- Glaucus atlanticus*, Fg 16.104, 926
- external appearance, Fg 16.104
- Gleba*, 926, 984, 985
- shell form, 923
- gliding, Ommastrephidae, 532
- Globicephala melas*, 538
- diet, 508
 - prey, 519
- Globiscala* in Australia, 816
- Globivenus*, 355, 358
- habitat, 358
 - lateral teeth, 358
- Globophilina*, 951
- glochidia, 12, 28
- Cucumerunio novaehollandiae*, 292
 - host attraction, 292
 - Hyridella depressa*, Fg 1.22
 - Hyridella drapeta*, 292
 - Hyriidae, Fg 7.6, 292, 298
 - morphology, Fg 7.6, 292
 - Palaeoheterodonta, Fg 7.6, 289
 - taxonomic value, 59
 - Unionidae, Fg 4.21
 - Unionoida, 296
- Glossaulax*, 791
- Glossidae, Fg 8.34, 351
- family treatment, 351
- Glossocardia*, Trapeziidae, 348
- Glossodoris*, 999
- radular teeth, Fg 16.10
- Glossodoris atromarginata*, 941, 1000
- Glossodoris rubroannulata*, Fg 16.83
- external appearance, Fg 16.83
- Glossodoris rufomarginata*, Fg 16.10, Fg 16.83, 1000
- radula, Fg 16.10, Fg 16.83
- Glossoida, 350
- description, 351
- Glossus humanus*, 352
- heart, 352
 - reproduction, 352
- Glossus lamarckii*, 352
- Glossus*, as fossils, 352
- Glossus sensu stricto*, 352
- Glossus moltkiana*, 352
- Glossus sanguineomaculata*, Fg 8.34, 351, 352
- Glossus vulgaris*, 352

INDEX

- Glycimeris*, Cretaceous, Tb 1.6
glycogenase, 364
Glycydonta
escape response, 305, 358
habitat, 358
Glycymerididae, Fg 6.6, 38
family treatment, 259
Glycymeris, 260
photoreceptors, 212
on sand plains, 38
sculpture, 259
Tertiary, 99
Glycymeris broadfooti
host to *Myochama*, 418
Glycymeris crebreiliratus
distribution, 260
Glycymeris dampierensis
endemic, 260
Glycymeris pectiniformis, 259
Glycymeris persimilis
endemic, 260
Glycymeris radians, endemic, 260
Glycymeris reevei, distribution, 260
Glycymeris striatularis
endemic, 260
Glyptodesma, Tb 1.6
Devonian, Tb 1.6
Glyptoleda, Permian, 97
Glyptonychia, Tb 1.6
Glyptopliceras, Triassic, 97
Glyptophysa, 84, 1074
affinities, 84
biogeography, 1056
copulatory organ, 1072
distribution, 84
in filters, 72
fossils, 84
origin, 1074
radiation, 1074
shell form, 64
shell sculpture, 1072
Trichobilharzia host, 69
Glyptophysa aliciae
copulatory organ, Fg 17.33
Glyptophysa concinna, Fg 1.71
shell, Fg 17.33
Glyptopupoides, 1084
distribution, 85
Glyptopupoides egregia, Fg 17.42
sculpture, Fg 17.42
shell, 1082
Glyptorhagada silveri
shell, Fg 17.69, 1112
Glyptozaria, 712, 860
Miocene, 712
Glyptozaria transenna
as fossils, 712
Glyptozoceras, Cretaceous, 99
Glyptophysa
Godwanan origins, 1074
Gnalt Shelf, Fg 1.95
Gnathodoridoidea, 990
Godiva, Fg 16.105, 1013
Godiva quadricolor, 941
Godiva sp., radula, Fg 16.105
Goldfuss, 237
gold-lipped pearl shell, 262
Golfingia
trochophore larvae, Fg 1.1
Golfingiidae, Fg 1.1
Gomphina, 360
diversity, 360
habitat, 358, 360
Gondwanaland model, 78
Gondwanan origin, 1057, 1075
Caryodidae, 86
Glacidorbidae, 84
Glacidorbis, 62
Planorbidae, 1056, 1074
Pomatiopsidae, 65, 83
Rhytididae, 1091
Smeagolidae, 1063
southern Australian bivalves, 222
Gondwanorbis, 84
Goniaeolididae, 1007
Goniatites, Carboniferous, 97
Goniatites granosus
Carboniferous, Fg 1.99
Goniocardium, as fossils, 336
Goniodoridella savignyi
feeding, 992
Goniodorididae, Fg 1.9, Fg 16.10,
Fg 16.19, Fg 16.72, Pl 35,
990
family treatment, 991
Goniodoris, 991, 992
Goniodoris atromarginata
painting, Fg 1.9
Goniodoris bennetti
painting, Fg 1.9
Goniodoris castanea, Fg 16.19, 992
egg masses, Fg 16.19
Goniodoris nodosa, 992
Goniodoris sp., feeding, 992
Goniophora, Tb 1.6
Devonian, Tb 1.6
Silurian, Tb 1.6
gonochorism
Architectonicoidea, 859
Bivalvia, 195
gonoduct fusion
Stylommatophora, 1049
gonopericardial system
Lepetelloidea, Fg 15.50
Goodingia, 633
Goolwa cockle, 347
Gordabyssia, 662
Gordonoceras, 491
Gorgoleptis, fertilisation, 631
gorgonians
as neomeniomorph prey, 151
Gould, August Addison, 7
Gouldia, 358
Gouldia australis, 357
Gouldia (Gouldiopa)
endemic subgenus, 357
Gouldoceras, 488
Gouldoceras synchronena
circulation, Fg 12.7
Gouldoceratidae, 490, 493
Gourmya, 712
Gourmya gourmyi
distribution, 712
head, mantle cavity, Fg 15.84
shell, Fg 15.83
grades of organisation
Opisthobranchia, Fg 16.1
Graftonoceras, 491
Grammatodon, Cretaceous, Tb 1.6
Grammatodon robusta
Cretaceous, Fg 1.100
Grammysia, Tb 1.6
Devonian, Tb 1.6
Grammysioidea, Tb 1.6
Grampus griseus, 508, 552
Granata, 681
distribution, 682
Granata imbricata
habitat, 681
radula, Fg 15.61
shell, Fg 15.61, 680
Grandeliacus, 861
Graneledoninae, 549
Granacorium, 360
endemic, 357
habitat, 358
sand coating, 301
sand on shell, 356
Granacorium indutum, 357
habitat, 360
Granosolarium, 861
gonochorism, 862
operculum, 861
spermiogenesis, 862
Granulina, 841
Granulina nympha
external appearance, Fg 15.167
granulocyte, Bivalvia, 210
Graphidula, Cretaceous, 99
Graptacme, Fg 10.14, 439
Graptacme aciculum
shell, Fg 10.14
Gray, John Edward, 7, 162, 196,
237, 639
grazing effect, intertidal algae, 30
Great Artesian Basin, Fg 1.95, 88
Great Barrier Reef, 33
Aplacophora, 145
green turtle, seagrass consumer, 38
greenlip abalone, fishery, 73, 669
Gregariella
byssal attachment, 253
Greilada, 993
Grey, Sir George, 9
Greyian fluvifauna
freshwater molluscs, 81
Greyian Province, Fg 1.89
Gricoploma, 410
Griffithsia, 972
Grimalditeuthidae, Fg 11.10,
Fg 3.26, 539
family treatment, 538
Grimalditeuthis, 539
external appearance, Fg 11.10
fin shape, Fg 11.10
Grimalditeuthis bomplandii, 539
external appearance, Fg 13.26
radula, Fg 13.26
Grimpella, 549
Grimpella thaumastocheir, Pl 21,
550
external appearance, Fg 13.35
hectocotylus, Fg 13.35
Gripoteuthis
prey, 545
Gripoteuthis glacialis, prey, 545
Grossouvrites, Cretaceous, 99
growth
Cephalopoda, 470
Conidae, 853
Idiosepiidae, 514
Loliginidae, 519
Polyplacophora, 174
Sepiidae, 508
growth rate
Enoploteuthidae, 521
Neritidae, 697
Onychoteuthidae, 524
growth rings
Architeuthidae, 528
growth to maturity
life history, 28
Gryphaeidae, Fg 6.14, Pl 12
family treatment, 269
on reef slope, 35
Gryphaeinae, 269
Gudeoconcha
Lord Howe Island, 1106
Gudeoconcha sophiae, 114
Guerangeria, Tb 1.6
Guianadesma sinuosum, 405
Guildfordia, 614
Gulella bicolor
dispersal, 1090
distribution, 1090
radula, Fg 17.50
shell, Fg 17.50, 1090
as snail predator, 1091
gulls, as molluscan predators, 43
Gunnarites
Cretaceous, 99
gut looping
Docoglossa, 642
Lottiidae, 642
Patellogastropoda, 642
Patelloidea, 642
Gyliotrachela, 1084
distribution, 85
limestone association, 1082
shell, 1082
Gyliotrachela australis, Fg 17.42
habitat, 1052
sculpture, Fg 17.42
Gyliotrachela ningbingia
shell, Fg 14.4
Gymnodorididae, Fg 16.78, 990,
993
family treatment, 994
Gymnodoris, 968, 994, 995
Gymnodoris okinawae
radula, Fg 16.78
Gymnodoris plebeia, Fg 16.78
external appearance, Fg 16.78
organisation, Fg 16.1
Gymnodoris striata, 967
Gymnomorpha, 1047, 1060, 1067
Gymnophila, 1060
Gymnoptera, 986, 989
Gymnosomata, 47, 606, 986
characters, 985
external appearance, 923
locomotion, 13
gymnosomes, 986
Gyraulus, 70, 1072
copulatory organ, 1072
distribution, 84
as fossil, 1058
fossils, 84
shell, 64, 1072
shell sculpture, 1072
vector of paramphistomes, 70
Gyraulus chapmani, as fossil, 1074
Gyraulus gilberti
Orthocoelium streptocoelium, 67
Gyraulus isingi, penis, Fg 17.33
Gyraulus meridionalis
shell, Fg 17.33
Gyraulus scottianus
Calicophoron calicophorum, 67
Gyraulus waterhousei
reproductive tract, Fg 17.33
Gyrineum, distribution, 801
diversity in Australia, 801
habitat, 801
protoconch, 802
Gyrocochlea curtisiana
shell, Fg 17.55
Gyrocochlea paucilamellata
pallial complex, Fg 17.56
reproductive anatomy, Fg 17.56
Gyrodos, Cretaceous, 99
Gyrodoma, Devonian, 95
Gyronema, Devonian, 95



Haasodonta,
affinities, 59
in Riechian fluvifauna, 81
habitat

Carditidae, 324
Crassostreinae, 272
Pectinidae, 277
Pinnidae, 265
Pteriomorpha, 249

habitat destruction
impact on pulmonates, 1054
and marine molluscs, 115

habitat modification, 107

habitat preferences
Polyplacophora, 175

habitats
Acochlidia, 959
ancestral Gastropoda, 605
Anomalodesmata, 219, 402
Basommatophora, 1052, 1067
Bivalvia, 5
Carinarioida, 804
Cephalaspidea, 943
Cephalopoda, 471
Cerithioidea, 709, 712
Cirrata, 545
Cocculiniformia, 654
Cocculinoidea, 610
Conoidea, 846
coral reef, Fig 1.27
Corbiculoidea, 352
Crassatelloidea, 325
diversity in Bivalvia, 218
Dreissenoida, 219
Eupulmonata, 1076
Heterodonta, 219, 301, 304
Lepetopsina, 648
Lucinoidea, 309, 310
Mactroidea, 336, 337
Nudibranchia, 990
Ostreoida, 269
Palaeoheterodonta, 219
Pandoroidea, 415
Patellogastropoda, 643
Pleurotomarioidea, 665
Protobranchia, 236
Pteriomorpha, 219, 249
Pulmonata, 1037
Scaphopoda, 437
Seguenziidae, 693
Solenoida, 304, 340, 341
Stromboidea, 766
Tellinoidea, 304, 342
Thecosomata, 980
Thracioidea, 408
Tridacnoidea, 332

Hadra, habitat, 1052

Hadra barneyi
external appearance, Fig 17.20
Hadra bipartita, Pl 32

Hadridae, 86

Hadroocorys, 794

haemocoel
Aglajidae, Fig 16.8, 925
Anaspidea, 925
Aplacophora, 147
Bivalvia, 203
Cephalaspidea, Fig 16.8, 925
Helicidae, Fig 17.11
Mollusca, 16
Nudibranchia, 925, 928
Opisthobranchia, Fig 16.8, 925
Pulmonata, Fig 17.11, 1041, 1044

haemocoel function
Bivalvia, 205, 206

haemocyanin, 16
Cephalopoda, 462
Coleoidea, 501

Gastropoda, 581
gastropoda, 624
Nuculidae, 239
oxygen carrying capacity, 527
Polyplacophora, 167
Protobranchia, 235
Pulmonata, 1047

haemocytes, Cephalopoda, 462

haemoglobin, 16, 326

Arcidae, 212, 256
Astartidae, 328
Carditidae, 324
Gastropoda, 581
Glycymerididae, 212
Heterodonta, 302
Lucinidae, 313
Planorbidae, 1047
Polyplacophora, 167
Pulmonata, 1047
Solemyidae, 243
sulphide-oxidation, 313
Vesicomyidae, 351

haemolymph
Polyplacophora, 167
Scaphopoda, 434

haemolymph sinuses
Scaphopoda, 435

Hainaspira, Cretaceous, 99

hairy tritons, 800

Halgerda aurantiomaculata,
Fig 16.82
external appearance, Fig 16.82

Halgerda willeyi, Pl 35

Halgerdidae, 997

Halimeda, 968, 970, 971

and Cyndrobullidae, 947

Halimeda macrolobata, 971

Haliotidae, Fig 1.16, Fig 1.79,
Fig 1.80, Fig 14.3, Fig 14.4,
Fig 14.9, Fig 14.13, Fig 15.15,
Fig 15.53, Pl 22, Tb 15.1

in Australia, 664, 667
catches, Fig 1.79
common names, 667
exhalant opening, 18
exploitation, 669
family treatment, 667
fisheries, 73
locomotor wave form, 611
pallial organs, 615
on reef conglomerate, 36
shell muscles, 613
State fisheries, Fig 1.80

Haliotis, 54, 581

in Australia, 667

cue for settlement, 54

diversity, 667

escape response, 612

fisheries, 73

fossil record, 88

as host of *Sabia*, 771

locomotion, 574

locomotor wave patterns, Fig 14.9

shell cleaning, 613

State fisheries, Fig 1.80

subradular organ, 630

torsion, 565

vascular system, Fig 15.15

Haliotis asinina, Pl 22

shell, 668

Haliotis cracherodi

pheromones, 635

Haliotis cyclobates

external appearance, Fig 14.4

spawning cycle, 591

Haliotis gabra, 6

Haliotis laevigata, Pl 22

catches, Fig 1.79

fishery, 73, 669

spawning cycle, 591

Haliotis roei, 668, 669

catches, Fig 1.79

fishery, 73, 669

spawning cycle, 591

spawning season, 24

Haliotis ruber

catches, Fig 1.79

external appearance, Fig 14.3

fishery, 73, 669

shell, Fig 15.53

Haliotis rufescens, radula, Fig 15.53

Haliotis spp.

economic importance, 73

Haliotis tuberculata

egg size, 634

nervous system,

Fig 1.16, Fig 14.13

Halioidea, 664

features, 610

Halistrepta, 410

Halistylinae, 679

description, 688

Halistylus, 688, 689

external appearance, 688

Halistylus pupoideus

head-foot, Fig 15.67

radula, Fig 15.67

Halixodes chitonis, 175

and *Cryptochiton porosus*, 188

Hall, Thomas Sergeant, 11

Halobates sericeus, 49

egg laying, Fig 1.53

Halobioidea, 268

Haloceras, 772

shell, Fig 15.125

Haloceratidae, 769

family treatment, 772

Haloginella, shell, 838

Haloginella mustelina

radular teeth, Fig 15.167

Haloginella mustellina

shell, Fig 15.167

Haloepa

Devonian, 95

Silurian, 95

Haminella, 955

Hamineobulla, 956

Hancock's organs, 956

radula, 956

shell, 956

Haminoea, Fig 16.3, Fig 16.16, 42,

586, 932, 935, 954–956, 959,

974

internal morphology, Fig 16.3

internalisation of shell, 573

nervous system, Fig 16.16

organisation, Fig 16.1

Haminoea crocata, 955

Haminoea navicula, 954

Haminoea simillina, Fig 16.5,

Fig 16.17, Pl 33

external appearance, Fig 14.7,

Fig 16.5

Hancock's organ, Fig 16.17

Haminoea zelandiae, Fig 16.11,

Fig 16.13, Fig 16.18, Fig 16.19

alimentary tract, Fig 14.26,

Fig 16.13

egg masses, Fig 16.19

gizzard plates, Fig 16.13

jaw plate, Fig 16.11

reproduction, Fig 16.18

stomach, Fig 14.26

Haminoidae, Fig 14.7, Fig 14.26,

Fig 16.5, Fig 16.11, Fig 16.13,

Fig 16.33, Figs 16.16–16.19,

Pl 33, 932

diet, 937

family treatment, 954

gizzard plates, Fig 16.13

gut, Fig 16.13

Haminoeoidea, characters, 954

Hamites, Cretaceous, 99

hammer oysters, 225, 262

Hanacuna, 325

Hancockia, 1003, 1004

Hancockia burni, Fig 16.89

external appearance, Fig 16.89

radula, Fig 16.89

Hancockia californica, Fig 16.17

rhizophores, Fig 16.17

Hancockiidae, Fig 16.17, Fig 16.89

family treatment, 1003

rhizophore, Fig 16.17

Hancock's organs, Fig 16.17, 918

Aglajidae, 952

Bullidae, 957

Bullinidae, 944

Cephalaspidea, 940, 943

Cylichnidae, 948

Haminoidae, Fig 16.17, 955

Haminoeoidea, 954

Hydatinidae, Fig 16.17, 945

nerves in *Aglaja inermis*, 931

Opisthobranchia, 932

Philinidae, 950

Retusidae, 949

Runcinidae, 958

Smaragdinellidae, 956

Hanleya, 165, 179, 180

habitat, 175

Hanleya hanleyi

digestive tract, Fig 3.8

Hanleya nagelfar, 179

Hanleya setulosum, 179

Hanleyella, 178

Hanleyidae, Fig 3.8, Fig 3.32, 161

family treatment, 179

Hapalochlaena, toxic bite, 16

Hapalochlaena fasciata

eggs, 549

Hapalochlaena lunulata, eggs, 549

Hapalochlaena maculosa, Pl 19,

500, 549, 550

brooding, 469

eggs, 549

external appearance, Fig 13.35

hectocotylus, Fig 13.35

neurotoxin, 500

parental care, 25

Haplorchis parataichui, Tb 1.2

Haplorchis pumilio, Tb 1.2

Haplorchis sprenti, Tb 1.2

Haplorchis vanissimus, Tb 1.2

Haplorchis yokogawai, Tb 1.2

Haplotrematidae, 1091

Harpa, 837, 838

diversity, 837, 838

egg mass, 838

as fossils, 838

prey, 838

Harpa armouretta

external appearance, Fig 15.166

radula, Fig 15.166

Harpa articularis

shell, Fig 15.166

Harpa major

egg capsules, Fig 15.166

Harpidae, Fig 15.166, Tb 15.1

family treatment, 837

on reef slope, 35

Harpinae, 837

characters, 837

Hartungia, 814

as fossils, 814

Hastula, 613, 850

alimentary tract, 850

characters, 850

diversity, 851

INDEX

- foot, 850
- prey capture, 850
- proboscis, 850
- in surf zone, 850
- Hastula cinerea*, foregut, Fg 15.175
- Hastula inconstans*
 - copulation, 850
 - locomotion, Fg 14.11, 574
- Hastula rufomaculata*
 - endemic, 851
- hatching, Argonautidae, 554
- hatching gland
 - Coleoidea, 470
- Haustator*, 718
- Haustellum*
 - diversity in Australia, 823
- Haustrum*, 822, 823
- Hawaii minuscula*, 1104
- head
 - Conoidea, 846
 - Emblandidae, Fg 15.107
 - Neogastropoda, Fg 15.162
 - Rissooidea, Fg 15.107
- head-foot, 565
 - Architectonicoidea, Fg 15.182, Fg 15.183
 - Campaniloidea, Fg 15.99
 - Cerithioidea, Fg 15.86, Fg 15.92
 - Heterobranchia, Fg 15.182, Fg 15.183, Fg 15.186
 - Ptenoglossa, Fg 15.150
 - Pulmonata, 1041
 - Pyramidelloidea, Fg 15.186
 - Rissooidea, Fg 15.105, Fg 15.106, Fg 15.108, Fg 15.110, Fg 15.111, Fg 15.114, Fg 15.115
 - Triphoroidea, Fg 15.150
 - Vanikoroidea, Fg 15.124
 - Xenophoroidea, Fg 15.128
- head-foot protrusion
 - Pulmonata, 1044, 1045
- head-foot retraction
 - Pulmonata, Fg 17.5, 1044
- Heard Island
 - Aplacophora, 145
 - Nacella macquariensis*, 647
- heart
 - Anomalodesmata, 401
 - Anomioidea, 280
 - Bivalvia, Fg 4.15, 210
 - Cephalopoda, 462
 - Cocculiniformia, 654
 - Coleoidea, 501
 - Fissurelloidea, 669
 - Gastropoda, 581
 - Heterodonta, 302
 - Mactroidea, 337
 - Myoidea, 363
 - Neritoidea, 694
 - Opisthobranchia, 928
 - Ostreoidea, 269
 - Patellogastropoda, 642
 - Pholadomyoidea, 406
 - Polyplacophora, Fg 3.11, Fg 3.12, 168
 - Proserpininae, 702
 - prosobranchs, 623
 - Pulmonata, 1044
 - Scaphopoda, 435
 - Trochoidea, 672
 - Veneroidea, 356
- heart, secondary
 - Opisthobranchia, 929
- heart autoregulation, Bivalvia, 210
- heart cockles, 328
- heart rates
 - Aplacophora, 147
 - Bivalvia, 211
- heart structure, 12, 16
- heavy metals, Pteriidae, 262
- Hebetodiscus*, 1100
- Hebeulima*, diversity, 817
- Hectocotylus*, 552
- hectocotylus, 51
 - Cephalopoda, 22
 - Coleoidea, 469, 501
 - Myopsida, 517
 - Octopoda, Fgs 13.35–13.37
 - Oegopsida, 520
 - origin of term, 552
 - Sepioidea, Fg 13.1, Fg 13.7, Fg 13.8
 - Teuthoidea, Fg 13.9, Fg 13.11, Fg 13.22
- Hedley, Charles, 9, 10, 77, 163, 196, 301, 432, 568, 569, 592, 1038
- Hedleya*, shell, 705
- Hedleya macleayi*, shell, Fg 15.79
- Hedleyella*, 81, 1093
- Hedleyella falconeri*, 1093
 - external appearance, Fg 17.52
- Hedleyoconcha*
 - affinities, 1057
 - habitat, 1052
- Hedleyoconcha delta*, 1098
 - radula, Fg 17.56
- Hedleytriphora*
 - diversity in Australia, 811
- Hedleytriphora innotabilis*
 - protoconch, Fg 15.148
 - shell, Fg 15.148
- Hedylopsidae, Fg 16.41
 - family treatment, 960
- Hedylopsis suecica*, Fg 16.41
 - external appearance, Fg 16.41
- Helcion*, 645
- Helcion pellucidum*, diet, 620
- Helcionella*, Cambrian, 89
- Helcionella terraustralis*
 - Cambrian, Fg 1.97
- Helcionelloidea, 89
- Heliacus*, 861, 862
 - colour, 861
 - diversity, 861
 - feeding, 862
 - as fossils, 862
 - hermaphroditism, 862
 - laboratory study, 862
 - operculum, 861
 - protandry, 862
- Heliacus cylindricus*
 - egg mass, 862
 - feeding, 862
 - spermatophores, 862
- Heliacus perrieri*, 862
- Heliacus trochoides*, feeding, 862
- Heliacus variegatus*
 - spermiogenesis, 862
 - underside of animal, Fg 15.183
- Helicarion*, Fg 1.61, Pl 32, 1106
 - distribution, 86
 - microhabitat, 1052
 - radula, Fg 17.63
 - water conservation, 1055
- Helicarion australis*
 - sperm ultrastructure, Fg 17.19
- Helicarion cuvieri*
 - reproductive tract, Fg 17.63
 - shell, Fg 17.63
- Helicarion sp.*
 - external appearance, Fg 17.20
- Helicarion virens*
 - eggs, Fg 1.20
 - lungworm, 1106
- Helicarionidae, Fg 1.20, Fg 1.61, Fg 14.7, Fg 17.1, Fg 17.3, Fg 17.19, Fg 17.20, Fg 17.63, Pl 32, Tb 1.5, 85, 1102
- affinities, 86, 1057
- defensive behaviour, 1055
- family treatment, 1105
- Gondwanan origins, 1057
- internalisation of shell, 573
- on Lord Howe Island, 113
- on Norfolk Island, 114, 1057
- Helicella obvia*
 - oxygen consumption, 1046
- Helicellidae, 1114
- Helicidae, Fg 1.77, Fg 14.9, Fg 14.13, Fg 17.8, Fg 17.11, Fg 17.14, Fg 17.15, Fg 17.19, Fg 17.71, Tb 1.5, 1113
 - family treatment, 1113
- Helicigona lapicida*
 - oxygen consumption, 1046
- Helicina orbiculata*, as pest, 702
- Helicinidae, Fg 15.77, Tb 1.5, Tb 15.1, 85, 610, 693, 694, 702
 - family treatment, 702
 - in Palaeozoic, 606
- Helicininae, 702
- Helicocranchia pfefferi*
 - ammonium, retention, 501
 - external appearance, Fg 13.28
- Helicodiscidae, Fg 17.57, Tb 1.5, 85
 - family treatment, 1100
- Helicodiscus*, 1100
- Helicoidea
 - description, 1113
 - gonoduct fusion, 1049
 - love darts, 1050
- Helicopelta rostricola*, 658
- Helicorbis*, 70, 1072
 - copulatory organ, 1072
 - distribution, 84
 - shell, 64, 1072
 - shell sculpture, 1072
- Helicorbis australiensis*
 - host of *Paramphistomum ichikawai*, 67
 - shell, Fg 17.33
- Helicostylinae, 1115
- Helicotoma*, Ordovician, 92
- Heliocidaris erythrogramma*
 - eulimid parasites, 817
- Heliopora*, 1008
- Heliopora coerulea*, 938, 1008
 - as food of *Doridomorpha gardineri*, Fg 16.96, 1008
- Helisalia*, 864
- Helisalia pallida*, 864
- Helisalia sucina*, 864
- Helix*, 1041
 - aestivation, 625
 - buccal mass, Fg 17.8
 - courtship, 24
 - heart action, 581
 - locomotor wave patterns, Fg 14.9
 - nervous system, Fg 14.13, Fg 17.14
 - phototaxis, 577
 - retractor muscles, 1041
- Helix aperta*, Fg 1.77
- Helix aspersa*, 55
 - circadian rhythm, 57
 - circumoesophageal ring, 1047
 - commercial breeding, 1114
 - external appearance, Fg 17.71
 - host of *Angiostrongylus cantonensis*, 69
 - human consumption, 1056, 1114
 - love darts, 1055
 - as pest, 1114
- plant pest, 71
- radula, Fg 17.71
- radula formula, 1043
- reproductive tract, Fg 17.71
- rhytidids as predators, 1093
- hermaphroditism, 23
- sperm ultrastructure, Fg 17.19
- water loss, Tb 17.1
- Helix pomatia*, 1114
 - circulation, Fg 17.11
 - haemocoel, Fg 17.11
 - haemocoelic septa, 1044
 - as human food, 1114
 - musculature, 1041
 - oxygen consumption, 1046
 - retina, Fg 17.15
- Helix simsoniana*
 - affinities, 1058
 - as fossil, 1058
- Helix tasmaniensis*
 - affinities, 1058
 - as fossil, 1058
- helmet shells, 794, 795
- Helminthochitoninae, 178
- Helminthoglyptidae, 1113
- Helminthope*, 960
- Hemiarthrum*, 179, 180
- Hemiarthrum setulosum*, 179
 - external appearance, Fg 3.32
 - habitat, 179
 - valves, Fg 3.32
- Hemicerithium*, 735
- Hemidonacidae, Fg 8.17
 - family treatment, 331
- Hemidonax*, 331
 - as fossils, 332
- Hemidonax arafurensis*, 332
- Hemidonax chapmani*, 332
- Hemidonax dactylus*, 332
- Hemidonax dixoni*, 332
- Hemidonax donaciformis*, 332
- Hemidonax pictus*, Fg 8.17, 332
- Hemifusus*, distribution, 832
- Hemiliostraca*
 - diversity, 817
 - jaws, 817
 - radula, 817
- Hemimeniidae
 - characters, 154
- Hemipecten forbesianus*, 277
 - musculature, 205
 - shell, Fg 6.18
- Hemistomia*, 63, 83
 - distribution, 755
 - sculpture, 752
- Hemitoma*, 671
 - shell, 669
- Hemitoma octoradiata*
 - radula, Fg 15.54
- Hemizyga*
 - Devonian, 95
- Hemizyga granifera*
 - Devonian, Fg 1.98
- Hennocquia*, Palaeozoic, 645
- hepatopancreas, Coleoidea, 500
- Herald*, 919
- herbivory, 1103, 1106
 - Bulloidea, 943
 - Cephalaspidea, 943
 - Columbellidae, 829
 - Haminoeidea, 943
 - Helicidae, 1113
 - Muricoidea, 820
 - Nassariidae, 831
 - pulmonate gut, 1043
 - pulmonates, 15
 - Runcinoidea, 943
 - Sacoglossa, 961
- Hercoglossa*, 493

- external appearance,
Fg 16.2, Fg 16.54
and plastids, 940
Hermaea bifida, 972
Hermaea cruciata
egg laying, 972
mating behaviour, 972
Hermaea variopicta, 972
Hermæidae, Fg 16.54, 969
family treatment, 972
Hermania, 951
hermaphroditic duct
Amphibolidae, 1048
Pulmonata, 1048
Siphonariidae, 1048
hermaphroditism, 277, 588, 1106
alternative, 214, 215
Amphiboloidea, 1067
Anomalodesmata, 214, 401
Architectonicoidea, 859
Basommatophora, 1067
Bivalvia, 20, 195, 214
and brooding, 214
Camaenoidea, 1112
Cionelloidea, 1081
Cocculiniformia, 654
consecutive, 214, 215, 633
Galeommatoidea, 214, 303
Heterodonta, 303
Limacoidea, 1102
Lymnaeoidea, 1069
multiple protandrous, 633
Neomeniomorpha, 152
Omalogyroidea, 864
Opisthobranchia, 20
Pandoroidea, 415
Patellogastropoda, 642
Pectinoidea, 214
pelagic molluscs, 48
Polyplacophora, 172
prosobranchs, 633
protandrous, 19, 23
Pulmonata, 20, 1037, 1048
Pyramidelloidea, 865
rhythmical consecutive, 19, 214
Rissoellidae, 633
Scaphopoda, 436
simultaneous, 23, 214
Siphonarioidea, 1067
Streptaxoidea, 1090
Tridacnoidea, 303, 332
Valvatoidea, 856
hermit crabs and Neritidae, 699
Heroidae, 1007
Hervella, 1015
Hervellinae, 1015
Hespererato, 788
Hesperella, Devonian, 95
Het Hapenvan Hoom, 6
Heterobranchia, Tb 14.1, Tb 15.1,
605, 606
affinities, 703
circulation pattern, 624
description, 854
eyes, 629
fertilisation, 631
functional kidney, 626
groups, 854
heart, 623
hermaphroditism, 633
modified euspermatozoa, 20
monophyly, 854
nerve ring, 628
nervous system, 628
origin, 940
sister group, 854
sperm morphology, 854, 936
status, 567
synapomorphies, 854
taxonomic history, 854
veliger, 22
Heterocardia, 337
Heterochitoninae, 184
heterochrony, 639
heterodont system, Fg 4.6
Heterodonta, 225, 226, 301
affinities, 305, 306
Australian higher taxa, Tb 8.1
behaviour, 305
biogeography, phylogeny, 305
characters, 301
circulation, 302
classification, 306
description, 301
distribution, 305
ecology, 304
economic significance, 305
embryology, development, 303
excretion, 303
external features and shells, 301
feeding and digestion, 302
fossil record, 306
history of discovery, 301
life history, 304
morphology and physiology, 301
musculature and locomotion, 302
natural history, 304
orders, 306
reproduction, 303
respiration, 303
sense organs and nervous
system, 303
statocyst, 214
Veneroidea, 306
Heterodoridae, 1007
Heterodoris, 1007
Heterogastropoda, 566, 606, 808
Heteroglossa, 610
Heteroglypta, shell, 345
Heterololigo, shell, 517
heteromyarian condition, Fg 4.11
Heterophyes nocens, Tb 1.2
Heterophyidae, Tb 1.2, 68
Heteropoda, 606, 703, 804
affinities, 703
diversity, 804
feeding, 804
trematode cercariae, 49
Heteroschismoides, 444
Heterostropha, 606, 854
Allogastropoda plesiomorphies,
854
paraphyly, 854
status, 567
Heteroteuthinae, 510, 511
Heteroteuthis, 511
bioluminescent ink, 474
luminescent organs, 511
Heteroteuthis hawaiiensis
photosensitive vesicles, Fg 11.20
Heteroteuthis serventyi, 511
arm crown, Fg 13.7
external appearance, Fg 13.6
hectocotylus, Fg 13.7
male tentacular club, Fg 13.7
heterourethry, 1086
Sigmurethra, 1086
Heterozostera, 39, 968
Heterurethra, 1108
Hexabanchidae, Fg 16.9,
Fg 16.81, 997
family treatment, 997
Hexabanchus, 997, 998
Hexabanchus sanguineus,
Fg 16.81, 934, 941, 997
external appearance, Fg 16.81
radula, Fg 16.81
swimming, Fg 16.9, 574, 925
Hexaplex trunculus
Tyrian purple, 823
Hiatella, 370, 371
boring, 363
byssus, 371
shell, 370
Hiatella angasi, 370
Hiatella arctica, 370
distribution, 370
Hiatella australis, 370, 371
distribution, 370
habitat, 370
shell, Fg 8.44
Hiatella subalta, as sportellid, 370
Hiatelloidea, Fg 8.44
family treatment, 370
genera, 370
Hiatelloidea, 226
description, 370
nacre, 202
Hiatula, 345
Hina, 360
Hinds, Richard, 7
Hinea, 722, 724
bioluminescence, 722, 724
distribution, 724
Hinea brasiliensis, 724
shell, Fg 15.91
hinge, 317
Anomalodesmata, Fg 9.1, 398
Bivalvia, 198
Corbiculoidea, Fg 8.35, Fg 8.36
Galeommatoidea, Fg 8.8
Limopsoidea, 258
hinge dentition, 339
Arcoidea, 200, 253
Arcoidea, 254
Arcticoidea, 302, 348
Bivalvia, 199, 200
Cardioidea, 201, 328
Carditoidea, 201, 322
corbiculoid type, 302
Corbiculoidea, 201, 352
Crassatelloidea, 201, 325
Cyamioidea, 318
cyrenoid type, 302
Cyrenoidea, 201
Galeommatoidea, 316
Glossoidea, 351
Heterodonta, 200, 301
Hiatelloidea, 370
Hippuritoida, 301
Limopsoidea, 258
lucinooid type, 302
Lucinoidea, 201
Mactroidea, Fg 8.22, 336
Myoidea, 200, 301, 362
Myoidea, 363
Mytiloidea, 250
notation systems, 200
Nuculoidea, 200
Palaeoheterodonta, Fg 7.2, 289,
290
Solenioidea, 340
Tellinoidea, 342
terminology, Fg 4.6, 200
Tridacnoidea, 332
Trigonoidea, 200, 295
Unionoidea, 296
Veneroidea, 301
Veneroidea, Fg 8.37, 201, 355
hinge lamellae, Bivalvia, 200
hinge orientation
Tridacnoidea, 332
hinge plate
Bivalvia, Fg 4.4, Fg 4.6
Heterodonta, Fg 4.6
Petricolidae, Fg 8.39
Hinnites, 275, 277
Hipponicidae, Fg 1.46, Fg 15.123,
Tb 15.1, 44, 637, 769, 868
family treatment, 770
genera, 771
Hipponicoida, 769
consecutive hermaphroditism,
633
Hipponix, 770, 771
Hipponix australis
sex reversal, 588
Hipponix conicus, 771
brooding, 25
protandrous hermaphroditism, 23
Hippopodiidae, as fossils, 326
Hippopus, 332, 333, 336
ancestry, 336
as fossils, 336
generic characters, 332
hyaline organs, 332
mantle, 332
Hippopus hippopus, 332
ctenidia, 332
mariculture, 75
shell, Fg 8.20
Hippopus porcellanus, 332
Hippuritoida, 226, 306
Hirtoscala in Australia, 816
Histiotethidae, Fg 1.54, Fg 11.6,
Fg 11.9, Fg 11.10, Fg 11.25,
Fg 13.18, 529
as architeuthid prey, 528
family treatment, 528
Histioteuthis, 49
external appearance,
Fg 11.9, Fg 11.10
fin shape, Fg 11.10
mantle, 528
photophores, Fg 11.6
Histioteuthis atlantica, 529, 530
distribution, 530
Histioteuthis bonnellii
webbing, 529
Histioteuthis bonnellii corpuscula
distribution, 530
external appearance, Fg 13.18
Histioteuthis celestaria pacifica, 530
depth range, 529
Histioteuthis dofleini, 530
distribution, 530
Histioteuthis macrohista, 530
radula, Fg 13.18, 529
webbing, 529
Histioteuthis meleagroteuthis, 529
distribution, 530
Histioteuthis miranda, 528, 529
adult, Fg 1.54
beak, Fg 11.25
depth range, 529
distribution, 530
eggs, 529
external appearance, Fg 13.18
larva, Fg 1.54
history of discovery
Anomalodesmata, 397
Aplacophora, 145
Arcoidea, 254
Bivalvia, 195
Cephalopoda, 452
Coleoidea, 499
Columbellidae, 827
Conidae, 852
Corbiculoidea, 352
Gastropoda, 568
Heterodonta, 301
Lucinoidea, 310
Mollusca, 6
Opisthobranchia, 919
Palaeoheterodonta, 289
Pleurotomariidae, 665
Polyplacophora, 161
Protobranchia, 236
Pulmonata, 1038
Scaphopoda, 431
Trochoidea, 671
Holcostoma, 722

INDEX

- holobranchial gills, Fg 3.2, Fg 3.13
- Holocene
- Angariinae, 675
 - Arcidae, 256
 - Cerithiidae, 712
 - Corbulidae, 366
 - Dialidae, 714
 - fossil record, 101
 - Margaritinae, 683
 - Skeneidae, 691
 - Trochidae, 680
- Holohepatica, 990
- Holologica*, distribution, 811
- holopelagic gastropods, 46
- Janthinidae, 813
- holoplankton, 46
- holoplanktonic molluscs, 980
- Atlantidae, 804
 - carbonate recycling, 49
 - Carinariidae, 804, 806
 - Carinarioidae, 804
 - distribution, 49
 - Pterotracheidae, 804
 - swarming, 49
- Holopoda, 1060
- Sigmurethra, 1086
- Holopodops, 1060
- Sigmurethra, 1086
- Holothuria
- as eulimid hosts, 623
 - as muricid prey, 823
 - as tonnid prey, 803
- Holothuria cinerascens*
- as prey of *Tonna*, Fg 15.144
- Hombon, Jacques Bernard, 7, 1038
- home range, Octopodidae, 471
- home site
- Polyplacophora, 175
 - Scutellastra flexuosa*, 646
- homing behaviour, 577
- Acanthopleura gemmata*, 187
 - Polyplacophora, 175
- Homiodorididae, 997
- homomyarian condition, Fg 4.10
- hood, Nautilidae, Fg 12.11
- hook sacs, 986
- Hooker, Sir Joseph, 77
- hooks, Cephalopoda, 457
- Hopkinsia*, Pl 35, 991
- feeding, 992
- Hoplodoris nodulosa*, Fg 16.82
- external appearance, Fg 16.82
 - larval development, 27
- Hormosira banksii*
- effects of epibiota, 44
 - as epibiont, 44
- Hormotoma*, Ordovician, 92
- Hormotomina*, Devonian, 95
- Homyzyga*, Devonian, 95
- hosts
- hyiid glochidia, 293
 - Myochamidae, 418
- Houtman Abrolhos
- Angariinae, 675
- Hoyle's organ, Fg 11.24
- Hull, A.F.B., 163
- Humilaria*, 358
- Humphrey, Adolarius, 8
- Humphrey, George, 6, 8
- Humphreyia*, 413
- adductor muscles, 413
 - shell, 413
- Humphreyia gigantea*
- distribution, 415
- Humphreyia strangei*
- distribution, 415
 - as fossils, 415
 - internal morphology, Fg 9.12
 - shell, Fg 9.11
- Hunter, John, 6
- Hutton, W., 77
- Huxley, Thomas Henry, 7, 919
- Hyalidae, 752
- hyaline organs, 332
- Hyalinoecia* tubes, as food, 659
- Hyalocylis striata*, Fg 16.62
- shell, Fg 16.62
- Hyalogyra*
- habitat, 856
 - off New Zealand, 856
- Hyalogyrina*
- habitat, 856
 - off New Zealand, 856
- Hyalogyrinidae, 856
- Hyalopecten*, depth range, 277
- Hyaloteuthis*, light organs, 532
- Hyaloteuthis pelagica*
- distribution, 533
- Hyatina pallida*, foregut, Fg 15.168
- Hybochelus*, distribution, 681
- Hyatina*, 924, 927, 932, 934, 936, 945, 948
- organisation, Fg 16.1
- Hyatina albocincta*, 945
- Hyatina amplustre*, 937, 945
- Hyatina physis*, Fg 16.6, Fg 16.7, Fg 16.17, Fg 16.23, 937, 945
- epidermal glands, Fg 16.7
 - external appearance, Fg 16.23
 - Hancock's organ, Fg 16.17
 - mantle cavity, Fg 14.17, Fg 16.6
 - organisation, Fg 16.1
 - repugnatory glands, Fg 16.7
 - shell, Fg 16.23
 - stomach, Fg 14.26
- Hyatina velum*, 945
- Hyatinidae, Fg 14.17, Fg 14.26, Fg 16.6, Fg 16.7, Fg 16.17, Fg 16.23
- characters, 943
 - family treatment, 945
- Hydrobia*, as pyramidellid host, 867
- Hydrobia neglecta*, 620
- Hydrobia ulvae*, 620
- Hydrobia ventrosa*, 620
- Hydrobiidae, Fg 1.48, Fg 1.70, Fg 1.91, Fg 15.25, Fg 15.111, Tb 1.4, Tb 15.1, 755
- affinities, 746
 - Australian genera, 63
 - in caves, 112
 - conservation status, 64
 - diversity in springs, 64, 107
 - environmental vulnerability, 755
 - family treatment, 752
 - generic groups, 63
 - genetic differentiation, 592
 - in inland waters, 62, 63, 83
 - on Lord Howe Island, 114
 - oviduct, 745
 - probable extinctions, 107
 - radiation, 82
 - restricted distributions, 592
 - in sink holes, 755
 - subterranean faunas, 755
 - taxonomic groups, 83
- Hydrobioidea, 752
- Hydrocena monterosiana*
- feeding, 701
- Hydrocenidae, Fg 15.76, Tb 1.5, Tb 15.1, 85, 610, 693, 694
- family treatment, 701
- hydrochloric acid, shell boring, 622
- Hydrococcidae, Fg 15.118, Tb 15.1
- in brackish water, 62
 - family treatment, 763
- Hydrococcus*, 763
- density, 41
 - as fossils, 763
 - opportunism, 41
- Hydrococcus brazieri*, 763
- external appearance, Fg 15.118
 - habitat, 763
 - mantle cavity, Fg 15.118
 - operculum, Fg 15.118
 - penis, Fg 15.118
 - radula, Fg 15.118
 - shell, Fg 15.118
- Hydroginella*, 841
- hydroids
- as dotid prey, 1004
 - as embletoniid prey, 1016
 - as flabellinid prey, 1012
 - as glaucid prey, 1013
 - as neomeniid prey, 149
 - as scyllaeid prey, 1005
- hydrological indicators
- Thecosomata, 980
- hydromedusae
- as larval predators, 53
- Hydromyles*, 989
- Hydromyles globulosa*, Fg 16.70, 986, 989
- brooding, 936
 - external appearance, Fg 16.70
- Hydromylidae, Fg 16.70, 986
- family treatment, 989
- hydrostat, muscular, 573
- hydrostatic skeleton
- Bivalvia, 210
 - Gastropoda, 573
 - Opisthobranchia, 925
 - Pulmonata, 1041, 1044
- Hydrozoa
- as columbellid prey, 829
 - as neomeniid prey, 151
- Hygromiidae, 1114
- Hyolitha, phylogeny, 5
- Hyotissa*, 269, 270
- distribution, 270
 - shell, 269
- Hyotissa hyotis*, Pl 12, 269, 270
- distribution, 270
 - internal morphology, Fg 6.14
 - shell, Fg 6.14
- Hyotissa numisma*, distribution, 270
- Hypermastus*, diversity, 817
- Hyperoodon ampullatus*, 543
- Hyperoodon planifrons*, 538
- hypoathroid nervous system, Fg 15.17, 628
- Caenogastropoda, 628
 - Neritopsina, 628
 - Patellogastropoda, 628
 - Vetigastropoda, 628
- hypobranchial gland, Fg 14.1, 577
- Fimbriidae, 314
 - function in Janthinidae, 814
 - Marginellidae, Fg 15.168
 - Mitridae, 842
 - Muricidae, 822
 - Muricoidea, Fg 15.155, 820
 - Neogastropoda, Fg 15.155, Fg 15.168
 - Neritidae, 696
 - Scissurellidae, 666
 - Turbinellidae, 825
- hypobranchial secretion
- Neogastropoda, 808
 - Ptenoglossa, 808
 - Volutidae, 835
- hypodermic insemination
- Sacoglossa, 934
- hyponomic sinus
- Nautiloida, Fg 12.3, 488
- hypoplax
- Martesiinae, 375
 - Pholadidae, Fg 8.45, Fg 8.48
- Hypotrochus*, 735
- Hypotrochus semiplicatus*, 737
- Hypoturrillites*, Cretaceous, 99
- Hypselodoris*, Fg 16.10, 1000
- radular teeth, Fg 16.10
- Hypselodoris festiva*, Fg 16.19
- egg masses, Fg 16.19
- Hypsogastropoda, Tb 15.1, 819
- affinities, 703
 - groupings, 610
 - relationships, 610
 - taxa, 703
- Hyridella*, 61, 298
- breeding season, 292
 - brooding period, 24, 292
 - distribution, 59, 82, 298
 - glochidium, 59
 - in fluvifauunulae, 81
- Hyridella australis*, 298
- larval release, 25
 - osmoregulation, 291
 - parasitism, 292
 - shell, Fg 7.9
- Hyridella depressa*, Fg 1.66, 298
- glochidium, Fg 1.22, Fg 7.6
- Hyridella drapeta*, 196, 222, 292, 298
- development, 292
 - glochidial activity, 24
 - host species, 293
 - shell, Fg 7.1
- Hyridella glenelgensis*, 65, 110, 298
- size, 59
 - threats, 61
- Hyridella menziesi*, 61
- Hyridella moretonicus*, 110
- Hyridella narracanensis*, 298
- Hyridellinae, 59
- Hyriidae, Fg 1.22, Fg 1.66, Fg 4.6, Fg 7.1, Fg 7.2, Fg 7.5, Fg 7.6, Fg 7.9, Tb 1.4, 61, 226, 289, 296
- biogeography, 82
 - as bioindicators, 298
 - diversity, 107
 - effects of salinisation, 61
 - family treatment, 297
 - fossils, 82
 - glochidium, Fg 1.22
 - habitat preferences, 60
 - inland waters, 59
- Hysterocheras*, Cretaceous, 99
- 
- Ianthina*, 814
- Ianthinopsis*, Devonian, 95
- Idioctopodidae, 544
- Idiohamites*, Cretaceous, 99
- Idiosepiidae, Fg 13.8, Pl 18
- family treatment, 514
- Idiosepius*, 509
- life span, 514
- Idiosepius notoides*, Pl 18, 514
- external appearance, Fg 13.8
 - hectocotylus, Fg 13.8
 - radula, Fg 13.8, 514
- Idiosepius paradoxus*, 514
- diet, 514
 - hectocotylus, Fg 13.8
- Idiosepius pygmaeus*, 514
- egg laying, Fg 13.8
- Ilbia*, 941, 959

- Ilbia ilbi*, Fg 16.38, 959
external appearance, Fg 16.38
- Ilbiidae, Fg 16.38
family treatment, 959
- Ildica*, 958
- Iliona*, 310
- Illex argentinus*
fishery, 476
- Illex illecebrosus*, 49
captive study, 533
egg mass, 469
migration, 471
prey capture, 502
- Illicinae, 532
- Ilyanassa obsoleta*, 54
veliger, 51
- Imbricariinae, 841
- Imitoceras*
Carboniferous, 95, 97
- imposex
Buccinidae, 827
Muricidae, 823
Nassariidae, 831
and tributyltin, 76
- Inaequidens*
Ordovician, Tb 1.6, 92
- incertae sedis*
Opisthobranchia, 956
superfamily, 959
- Incirrata, description, 546
- Incisura*, 666
- incubation
Lophinae, 272
Ostreinae, 270
- incubation period
Achatinidae, 1089
Argonautidae, 554
Conidae, 853
Cypraeidae, 783
Cystopeltidae, 1107
Epitoniidae, 816
Harpidae, 838
Limacidae, 1102
Melongenidae, 832
Milacidae, 1103
Olividae, 837
Sepioidae, 511
Terebridae, 850
Testacellidae, 1108
Zonitidae, 1104
- indicator species, 106
- indirect development
Gastropoda, 637
- Indogrammatodon*
Cretaceous, Tb 1.6
- Indogrammatodon robusta*, Tb 1.6
- Indoplanorbis exustus*
vector of schistosomes, 70
- Indo-West Pacific affinities
northern Australian bivalves, 222
- Inella*
diversity in Australia, 811
- Inella spina*
protoconch, Fg 15.148
shell, Fg 15.148
- infrabranchial chamber
Bivalvia, Fg 4.5, 203
and brooding, 214
Heterodonta, 303
lamellibranch, Fg 4.5
Lucinidae, Fg 8.3
Nuculoida, Fg 5.1
Pholadidae, Fg 8.45
Protobranchia, Fg 4.5
Solemyoida, Fg 5.1
Teredinidae, Fg 8.51
- infula, Endocerida, Fg 12.5, 495
- Inglisella*, distribution, 846
- inhalant aperture, Chamidae, Fg 8.1
- inhalant current
Arcoidea, 217
Cardioidea, 306
Crassatelloidea, 306
Galeommatoidea, 217, 306
Lucinoidea, 306
Protobranchia, 217
Pteriomorpha, 217
- inhalant siphon
Arcoidea, 204
Fimbriidae, 309, 313
Muricoidea, 820
prey capture, 209
Trogonioidea, 204
- Iniotheuthis*, 511
- Iniotheuthis stenodactyla*, 511
- Iniotheuthis tasmanica*, 511
- ink
Cephalopoda, 474
function in Cephalopoda, 51
function in Coleoidea, 501
Gymnosomata, 48
Heteroteuthis, 474
- ink gland, Coleoidea, 501
- ink sac
Cephalopoda, 451, 474
Cycloteuthidae, 525
- Inkaba*
distribution, 689
- Innesoconcha*, 1106
Lord Howe Island, 1106
- Inoceramus*
Cretaceous, Tb 1.6, 99
Jurassic, 97
- Inoceramus carsoni*
Cretaceous, Fg 1.100
- Inopinodon*, 944
- Inquisitor*, 848
shell, 848
- insemination, hypodermic
Sacoglossa, 934
- insertion plates, Fg 3.4
- integument
Neomeniomorpha, 151
- intercalary cells
Lucinidae, Fg 8.3, 313
Lucinoidea, Fg 8.5
Solemyidae, Fg 5.11, 243
Thyasiridae, Fg 8.5
- intertidal distribution
Lottiinae, Fg 15.41
Patelloidinae, Fg 15.41
- intertidal sand beaches, 37
- intestinal passage rate
Agriolimax, 1044
- intestine
Cocculiniformia, 654
degree of coiling, 621
length and diet, 621
- intracellular digestion
Cephalopoda, 460
Gastropoda, 586
- intraembolic proboscis
formation, 619
- intrapigmentary ocellus, Fg 3.20
Polyplacophora, 171, 172
- intraspecific competition
on rocky shores, 31
- intritacalx
Bursidae, 794
Fissurellidae, 669, 671
Muricidae, 822
- introduced taxa
Achatina fulica, Fg 17.21,
Fg 17.49, 1051, 1055, 1087,
1089
Agriolimax reticulatus, 1042
Arion, 55
Arion ater, 1100
Arion hortensis, 1100
- Arion intermedius*, 1100
- Arionidae, Fg 17.58
- Arionoidea, Fg 17.58
- Asterias amurensis*, 115
- Austropelea viridis*, 64, 67
- Batillaria australis*, 722
and biological control, 1090
- Bradybaena similis*, Fg 17.20,
Fg 17.22, Fg 17.72, 1055,
1056, 1113, 1115
- Bradybaenidae*, Fg 17.20,
Fg 17.72
- Cernuella virgata*, 57, 1055
- Cionella lubrica*, 1042
- Cochlicella barbara*, Fg 17.71
and conservation, 109
- Crassostrea gigas*, 80, 115
- Deroceras*, 55
- Deroceras panormitanum*,
Fg 17.59
- Deroceras reticulatum*, Fg 17.59
distribution, 80
effects on native taxa, 115
Ena montana, 1085
- Enidae, 1085
- eradication, 1090
- Euconulus fulvus*, 1105
- Ferrussacia folliculus*, Fg 17.46,
1087
- Gastrocopta pediculus*, 1082
- Gastrocopta servilis*, 1082
- Godiva quadricolor*, 941
- Gulella bicolor*, Fg 17.50, 1087,
1090
- Helicidae, Fg 17.71, 1113
- Helicoidea, Fg 17.71, Fg 17.72
- Helix aperta*, 70
- Helix aspersa*, Fg 17.71, 55,
1055, 1056, 1113
- Janolus hyalinus*, 941
- Laevicaulis alte*, Fg 17.22, 1056,
1065
- Lamellaxis clavulinus*, 85, 1088
- Lamellaxis gracilis*, 1088
- Lehmannia flava*, Fg 17.59
- Lehmannia nyctelia*, Fg 17.59
- Limacidae, Fg 17.59, 1102
- Limacoidea, Fgs 17.59–17.61,
Fg 17.65
- Limax*, 55
- Limax maximus*, Fg 17.59, 1042
- Lord Howe Island, 1084
- Lymnaea auricularia*, 67
- Lymnaea columella*, 1056
- Lymnaea peregra*, 1070
- Lymnaea stagnalis*, 64, 67, 1042
- Lymnaea stagnalis*, 1070
- Maoricolpus roseus*, 80, 115
- Melanoides tuberculata*, 729
- Milacidae, Fg 17.60, 1102
- Milax gagates*, Fg 17.60, 1103
- Musculista senhousia*, 222, 253
- Mytilidae, 253
- Neilo australis*, 80
- Neilonellidae, 80
- Okenia plana*, 941
- Opeas pumilum*, 1088
- Ostrea lutaria*, 80
- Oxychilus*, Fg 17.61
- Oxychilus alliarius*, 1042
- Paphirus largillierii*, 80
- Physa acuta*, 62, 64
- Physella acuta*, 1075
- Physidae, 1074
- Planorbarius corneus*, 65, 84,
1072
- Planorbis campanulatus*, 65
- Pleurodiscus balmei*, 1084
- Polycera capensis*, 940, 941, 993
- Polycera hedgpethi*, 940, 941,
993
- Potamopyrgus antipodarum*, 64,
752
- Prosopaeas achatinaceum*, 1088
- Pseudosuccinea columella*, 64,
67, 70, 1070
- Pulmonata, Fg 17.22
- Pupilloidea, 1082
- Rhachistia histrio*, 1085
- Streptaxidae, Fg 17.50
- Streptostele musaecola*, 1090
- Subulina octona*, Fg 17.22, 1056,
1088
- Subulinidae, Fg 17.22, 1087
- Testacella haliotidea*, Fg 17.65,
55, 1056, 1108
- Testacellidae, Fg 17.65, 1102,
1107
- Theba pisana*, Fg 17.71, 85, 1114
- Thecacera pennigera*, 940, 941
- Theora lubrica*, 344
- Turritellidae, 80
- Vaginulus plebeius*, 1056, 1065
- Vallonia pulchella*, 1084, 1085
- Veneridae, 80
- Veronicellidae, Fg 17.22
- Zeacumantus subcarinatus*, 80,
593, 722
- Zonitidae, Fg 17.22, Fg 17.61,
1102, 1104
- Zonitoides arboreus*, Fg 17.22,
1056, 1104
- introvert and carnivory, 622
- Investigator*, 7
- Iotrigonia*, Cretaceous, Tb 1.6
- Iotula microcosmos*
shell sculpture, Fg 17.3
- Iravadia*, 752
in Australia, 752
- Iravadia australis*
reproductive system, Fg 15.110
radula, Fg 15.110
shell, Fg 15.110
- Iravadia densilabrum*
operculum, Fg 15.110
- Iravadia mahimensis*
distribution, 752
- Iravadia quadrasi*
distribution, 752
head-foot, Fg 15.110
protoconch, Fg 15.110
shell, Fg 15.110
- Iravadiidae*, Tb 15.1
in brackish water, 62
family treatment, 752
- Iredale, Tom, Fg 1.11, 10, 196,
236, 301, 499, 569, 1038,
1039
- iridescence, Oxynoidae, 963
- iridocytes
Cephalopoda, 454
Coleoidea, 500
- iridophores
Carinarioida, 804
cephalopod behaviour, 474
Cephalopoda, 454
Costasiellidae, 971
Plakobranchus, 967
- Iridoteuthis*, 511
arm crown, Fg 13.7
external appearance, Fg 13.6
hectocotylus, Fg 13.7
luminescent organs, 511
male tentacular club, Fg 13.7
- Irinoceras*
Carboniferous, 97
- Irinoceras tuba*, Permian, Fg 1.99
- Irus*, 360, 361
distribution, 360
diversity, 360
habitat, 358, 360
nestling, 358, 360
- Irusella*, 358
- Isanda*, 671
distribution, 689
habitat, 672
- Ischadium*, rectum, 251

INDEX

- Ischnochiton*, 44, 182, 183
Tertiary, 183
Ischnochiton adelaidensis, 183
Ischnochiton australis, 183
spawning, 173
Ischnochiton cariosus, 183
Ischnochiton contractus,
Fg 1.3, Pl 7
Ischnochiton crebristriatus, 183
Ischnochiton elongatus, Fg 3.34,
183
radula, Fg 3.10
Ischnochiton inca, 175
Ischnochiton (Ischnoplax), 177
Ischnochiton luticolens, 183
Ischnochiton maorianus, 164
Ischnochiton mawlei, 183
Ischnochiton mayi, 173, 174
Ischnochiton pilsbryi, 183
Ischnochiton (Radsilla), 177
Ischnochiton smaragdinus, 183
Ischnochiton subviridis
brooding, 174
Ischnochiton tateanus, 183
Ischnochiton tindalei, 183
Ischnochiton torri, Pl 7, 165, 182
Ischnochiton versicolor, 183
Ischnochiton virgatus, 183
Ischnochitonidae, Fg 1.3, Fg 3.10,
Fg 3.15, Fg 3.17, Fg 3.20,
Fg 3.23, Fg 3.34, Pl 7, 180
aesthetes, Fg 3.17
colouration, 164
embryo, Fg 3.23
family treatment, 180
intrapigmentary ocellus, Fg 3.20
metanephridia, Fg 3.15
Tertiary, 183
Ischnochitonika lasalliana
as parasite of chitons, 175
Ischnochitonina, 180
Ischnochitoninae, 182
Iselica, 869
Isidorella, 1074
affinities, 84
copulatory organ, 1072
distribution, 84
in filters, 72
as fossil, 1058
Gondwanan origins, 84, 1074
in mound springs, 64
shell, 65, 1072
shell sculpture, 1072
Isidorella newcombi
external appearance, Fg 17.33,
Fg 17.34
pulmonary cavity, Fg 17.33
radula, Fg 17.33
shell, Fg 17.33
tolerance of desiccation, 65
Isidorella, as fossil, 1074
Isocardia humanus, 352
Isoconcha integra, 318
isodont system, Fg 4.6
Isofilibranchia, 225, 249
Isognomon, 265
as ranellid prey, 800
Isognomon alatus, 265
Isognomon cf. vitrea
habitat, 265
Isognomon ephippium, 264, 265
byssus, 265
habitat, 265
host, *Sulcascaris sulcata*, 265
Isognomon isognomon, 262–264
habitat, 265
internal morphology, Fg 6.10
shell, Fg 6.10
Isognomon ephippium, 264
shell, Fg 6.10
Isognomonalatus
heart rate, 211
Isognomonidae, Fg 6.10, 225
family treatment, 264
Isolimea, 268
isomyarian condition, Fg 4.10
Isotriphora
diversity in Australia, 811
Isotriphora amethystina
operculum, Fg 15.148
protoconch, Fg 15.148
shell, Fg 15.148
iteroparity, 29
Argonautidae, 554
Bivalvia, 217
Cephalopoda, 51
Hyriidae, 218
Nautilus, 470
Ittibittium, 712
distribution, 712
head-foot, Fg 15.85
Ittibittium houbrieki
shell, Fg 15.85
- J**
- Jackson, Sydney, 11
Jacquinot, Capt. Charles Hector, 7,
1038
Janeia, as fossils, 241
Janeia silurica
earliest solemyid, 235
Janolidae, 1009
Janolus, 1009, 1010
organisation, Fg 16.1
Janolus australis, 1010
Janolus hyalinus, 941, 1010
Janolus ignis, 1010
Janszoon, Capt. William, 6
Janthina, 606, 813, 814
brooding, 637
distribution, 80, 594
flotation, 575
hermaphroditism, 633
jaws and feeding, 622
mantle cavity, 814
in neuston, 594
radula, Fg 15.151
sex reversal, 633
sinus, 814
Janthina balteata
paraspermatozoa, Fg 1.17
spermatozeugma, 21
Janthina exigua, Fg 1.49, 813
egg capsules, Fg 15.151, 814
oviparity, 814
Janthina janthina, Pl 24
brooding, 637
extrovert, Fg 15.151
sex reversal, 588
shell, Fg 15.151
viviparity, 814
Janthina pallida
egg capsules, 814
oviparity, 814
Janthinidae, Fg 1.17, Fg 1.49,
Fg 15.151, Pl 24, Tb 15.1,
813
associations, 814
egg masses, 49
family treatment, 813
flotation, 813
parasitic copepods, 49
in plankton, 47
siphonophore predator, 813
Janthinoidea, Tb 15.1, 703, 808
affinities, 808
description, 811
families, 813
feeding, 610
and Triphoroidea, 610
Japetella, 546
distribution, 546
Japetella diaphana
external appearance, Fg 13.32
ontogenetic descent, 546
radula, Fg 13.32, 546
Japonactaeon, 944
Jardinella, 63, 83
distribution, 755
radiation, 64
species affinities, 84
Jardinella thaunumi
radula, Fg 15.111
Jardinian fluvifaunula, molluscs, 81
Jardinian Province, Fg 1.89
jaw elements
Heterobranchia, Fg 15.179
Valvatoidea, Fg 15.179
jaw plates, 1000, 1002–1006,
10015–1017
Opisthobranchia, Fg 16.11
jaw rodlets
Chromodorididae, Fg 16.83
jaws, Fg 17.67, Fg 17.72, 1037
Coleoidea, 500
Heterobranchia, Fg 15.180
prosobranchs, 619
Valvatoidea, Fg 15.180
jelly gland, Fg 15.22
prosobranchs, 632
Jenneria pustulata
radula, Fg 15.131
jet propulsion
Cephalopoda, 451, 455
Coleoidea, 499, 500
efficiency of mechanism, 455
Loliginidae, 517
Nautilidae, 455
nervous control, 467
Notarchus punctatus, 925
Octopodidae, 549
Pectinoidea, 206
Solenoida, 305
Spirulidae, 504
Jetwoodsia, as fossils, 712
jewel box shells, 307
Joculator
distribution, 811
diversity, 811
Johania, 951
Johnmartinia, Ordovician, Tb 1.6
Johnson, R.M., 101
Johnston, Robert, 10
Jorunna funebris, Fg 16.82
radula, Fg 16.82
Jouannetia, 376
Jouannetia cumingii, 305, 374
external appearance, Fg 8.49
shell, Fg 8.49
Jouannetia globosa
external appearance, Fg 8.49
shell, Fg 8.49
Jouannetiinae, 376
Joubiniteuthidae, Fg 1.54,
Fg 13.27, 539
family treatment, 539
Joubiniteuthis portieri, 539
adult, Fg 1.54
dorsal view, Fg 13.27
larva, Fg 1.54
radula, Fg 13.27, 539
Jousseaumiella, 321
Jujubinus, 631
Jukes, Joseph, 7, 919
Julia, 937, 965
external features, 922
Julia exquisita, 965
Julia japonica, Fg 16.46, 965, 966
external appearance, Fg 16.46
Juliidae, Fg 16.46
family treatment, 964
Juliinae, 965
Jupiteria, 239
Jurassic, 97, 755
Arcoida, 253
Basommatophora, 1067
Cuspidarioidea, 424
marine transgressions, 91
Nautiloidea, 493
Rissooidea, 746
Scaphopoda, 437
Thracioidea, 408
Trigonia, 296
Valvatoidea, 856
Veneroida, 306
Jurassiphorus, 778
Juresanites, Permian, 97
Jutting, van Benthem, 352
Juvenichiton, 166
Juxtamusium, 275
- K**
- Kaiparapelta*, 662
Kaiparathina, 682
Kalentera, as fossil, 322
Kalinga ornata, 994
distribution, 994
external appearance, Fg 16.77
gills, 994
radula, Fg 16.77, 994
rhinophores, 994
Kalinginae, 993
characters, 994
Kallosinistrata, as fossils, 816
Kaloplocamus, 993, 994
bioluminescence, 994
Kaloplocamus acutus, Fg 16.75
external appearance, Fg 16.75
Kapala kengrahami, 827
Karagandites, Carboniferous, 97
Karumba Basin, Fg 1.95
karyotypes, Patellogastropoda, 643
Katelsysia, 304, 357, 360
distribution of fossils, 595
diversity, 360
endemic, 357
fishery, 221
habitat, 358, 360
Katelsysia peronii, 357, 358
Katelsysia rhytiphora, 44, 357, 358
fishery, 76
Katelsysia scalarina, 44, 357, 358
effects of epibiotia, 44
fishery, 76
Katharina tunicata, 184
as human food, 175
lifespan, 174
Katharininae, 184
Katylesia scalarina
hinge plate, Fg 4.6
shell morphology, Fg 4.4
Keber's gland
Bivalvia, 211
Keber's organs, 16
Keenia, Permian, 97
Kellia, 318
external appearance, Fg 8.8
Kelliella, 350
distribution, 350

- Kelliella miliaris*, 350
 Kelliellidae, 348
 family treatment, 350
 as prey of boring gastropods, 350
 kelp gull, as chiton predators, 184
 kelp shells, 683, 689
 Kentrodonidae, 997
Kereia, 360
 Kerguelen Island
 Struthiolariidae, 768
Kerguelenella lateralis
 development, 1069
 egg masses, 1069
 Kermadec Islands, 178, 695
 Hinea brasiliana, 724
 Kermadec Ridge
 Trochoidea, 673
 Kershaw, R.C., 1039
 Kesteven, Hereward, 568
 keyhole limpet, Pl 22, 669, 671
 keys
 aplacophoran subclasses, 149
 cephalopod orders, 503
 chaetoderm families, 151
 neomeniomorph families, 152
 scaphopod families/subfamilies, 438
 sepioid families, 504
 teuthoid families, 515
 keystone species, 106
 kidney function, prosobranchs, 625
 kidney primordia, 627
 kidneys
 Achatinoidea, 1087
 Anomalodesmata, 401
 Bivalvia, 203, 211
 Camaenoidea, 1112
 Coleoidea, 501
 Conoidea, 847
 digestion, giant clams, 303
 evolution in prosobranchs, 626
 Gastropoda, 581
 Helicoidea, 1113
 Heterodonta, 303
 Mollusca, 16
 Muricoidea, 820
 Myoidea, 363
 Orthurethra, 581, 1080
 Palaeoheterodonta, 291
 Partuloidea, 1085
 Patellogastropoda, 642
 Protobranchia, 211
 Pulmonata, 1037, 1045
 Pupilloidea, 1082
 Rhytidoidea, 1091
 role in reproduction, 625
 Stylommatophora, 581, 1080
 Succinoidea, 1108
 Vetigastropoda, 581, 625
Kimopegma
 in Upper Cambrian, 92
 King, Lieut. Phillip Parker, 7, 196, 568
Kionoceras, 491
Kitchinites, Cretaceous, 99
Kitikamispira, Devonian, 95
Kitikamispira ukalundensis
 Devonian, Fg 1.98
 kleptoplasty
 Costasiellidae, 972
 Elysiidae, 968
 Sacoglossa, 937, 961
 Kölliker bristles, 453
 Kölliker organs
 hatching octopods, 470
Knightoconus, Cambrian, 92
Kogia breviceps, 508, 543
Kogia simus, 508, 543
Kokenospira, Silurian, 95
Kolonella, shell, 867
Kondakovia, 524, 525
 Koninck, Laurent de, 8
Koolonella moniliformis
 shell, Fg 15.186
Kossmatia, Jurassic, 97
Kossmaticeras, Cretaceous, 99
Kossmaticeras brunnschweileri
 Cretaceous, Fg 1.100
 Krefftian fluvifauna, molluscs, 81
 Krefftian Province, Fg 1.89, 35
Kummelia, 368, 370
 in burrow, Fg 8.43
 shell, Fg 8.43
Kummelonautilus, 493
Kummelonautilus hendersoni,
 Fg 12.10, 99, 493
 Cretaceous, Fg 12.10
 Kuphinae, 362, 378
Kuphus, 362, 372, 376, 378
 characters, 378
 tube length, 378
Kuphus arenarius, 378
Kuphus dubia, 378
Kuphus polythalamia, 378
 external appearance, Fg 8.52
 habitat, 378
 shell, Fg 8.52
Kurilabyssia, 662
- 
- La Coquille*, 7, 1038
Labceras, Cretaceous, 99
 labial palps, 352
 Anomalodesmata, 399
 Mactroidea, 337
 Myoidea, 364
 Ostreoida, 269
 Pholadomyoidea, 406
 Solemyoidea, 241
 laboratory maintenance
 Aplacophora, 145
 Aplysiidae, 976
 Pulmonata, 1060
 labral commissure
 Patellogastropoda, 642
Labrocuspis, Devonian, 95
 Lacaze-Duthiers, H., 431
Lacuna, 738
 Lacuninae
 in Australia, 739
 distribution, 739
Laemodonta, 1078
 genital ducts, 1078
 habitat, 1078
Laetifactor, in Australia, 686
Laevicardium, 331
 heart, Fg 4.16
Laevicaulis alte, Fg 17.22, 1056, 1065
 as *Angiostrongylus cantonensis*
 vector, 1056
 distribution, 1065
 external appearance, Fg 17.28
 jaw, Fg 17.28
 radula, Fg 17.28
 reproductive system, Fg 17.28
Laevicirce, 358
Laevidentaliidae, Fg 10.16
 family treatment, 442
 as fossils, 437
Laevidentalium, 442
Laevidentalium caudani, 442
Laevidentalium crocinum
 shell, Fg 10.16
Laevidentalium erectum, 443
 depth range, 437
Laevidentalium largicrescens, 442
Laevidentalium leptoskeles, 442
Laevidentalium lubricatum, 442, 443
Laevidentalium species, Fg 1.3
Laevilitorina, 738
 distribution, 739
Laevilitorininae, distribution, 739
Laeviscalia
 in Australia, 816
Laevitrigonia lineata, Tb 1.6
 Laginiopsidae, 986
Laginiopsis trilobata, 926, 986
 lagoons
 freshwater, 41
 marine, 41
Lahillia
 as fossils, 328
 Tertiary, 99
Lahillia australica
 Tertiary, Fg 1.101
 Lahilliidae
 as fossils, 328
 Lamarck, Jean Baptiste de, 237, 337, 504, 549, 568, 1038
Lambis, 766, 768
 habitat, 768
 locomotion, 574
Lambis chiragra
 distribution, 768
 habitat, 768
 locomotion, righting response, Fg 14.10
 shell, Fg 15.121
Lambis crocata, distribution, 768
Lambis lambis, Pl 25, 768
 distribution, 768
 fisheries, 768
 in middens, Fg 1.36
Lambis scorpius, distribution, 768
Lambis truncata
 distribution, 768
 habitat, 768
Lamellaria, 787, 789, 790
 development, 787
 egg capsule, 635, 636
 external appearance, Fg 15.133
 internalisation of shell, 573
 radula, 786
 radular function, 583
 shell muscles, 613
Lamellaria australis, Pl 26
Lamellaria ophione
 shell, Fg 15.133
Lamellaria perspicua, 789, 790
 echinospira larva, Fg 15.30
 egg capsule, 787
 external appearance, Fg 14.7
 Lamellariaceae, 786
 Lamellariidae, Pl 26, 614, 774
 hermaphroditism, 633
 prostate gland, 632
 Lamellariinae, 787
 Lamellarioidea, 786
Lamellaxis clavulinus, 85, 1088
 radula, Fg 17.47
 reproductive system, Fg 17.47
 shell, Fg 17.47
Lamellaxis gracilis, 1088
 shell, Fg 17.47
 Lamellibranchia, 5, 225
 lamellibranchs
 relationship, protobranchs, 235
 Lamellidorididae, 992
Lamellinucla, 237
Lamellinucla pyrenoides
 as fossils, 239
Lamelliscula
 in Australia, 816
 Lametilidae, characters, 239
 Laminariales
 substrata for limpets, 644
 Lampadioteuthinae, genera, 520
Lampadioteuthis, 520
Lampeia, 408
 Lancinae, 1071
 land clearance
 effects on molluscs, 109
Janice, 937
Lanistina
 in ascidian tests, 253
 mantle fusion, 251
 style, 251
Lantana on Norfolk Island, 114
 lantern shells, 410
Laona, 951
Lapinura, 958
 Larapintine Sea, Fg 1.96
 Nautiloidea, 493
Larina, 62
 affinities, 82
 distribution, 707
 endemism, 707
 shell, 707
Larina strangei, 707
 affinities, 65
 distribution, 707
 shell, Fg 15.81, 707
 larvae
 anthropogenic effects, 54
 Bivalvia, 216
 Caenogastropoda, Fg 15.27, 637
 Doratopsis, 532, 533
 echinospira, Fg 15.30, 27
 glochidia, 12, 28
 hydrodynamic entrapment, 39
 lasidium, 296
 Littorinoidea, Fg 15.27
 metamorphosis, 54
 mortality in estuaries, 43
 paralarva, 502
 Patellogastropoda, 637
 pericalymma, 148
 predation by meiofauna, 43
 prosobranchs, 637
 rhynchoteuthion, 502, 532
 Scaphopoda, Fg 10.12
 stenocalymma, 436
 teleplanic, 39, 52
 trochophore, Fg 14.34
 veliger, Fg 14.35
 vertical migration, 637
 larval development
 Aplacophora, Fg 2.4
 Mollusca, 1
 Opisthobranchia, 936
 pelagic molluscs, 48
 Polyplacophora, Fg 3.24
 larval dispersal
 biogeography, 592
 Caenogastropoda, 637
 Cypraeidae, 36
 Tonnoidea, 637
 larval flotation, 638
 larval growth
 effect of temperature, 54
 quality of diet, 53
 larval life
 Donacidae, 347
 Gastropoda, 592
 larval life span, 156, 277, 345, 368, 416
 Anomalodesmata, 401
 Conidae, 853
 Epitoniidae, 816
 Ranellidae, 800
 Scaphopoda, 436

INDEX

- larval morphology, Fg 4.21
Palaeoheterodonta, Fg 4.21
Pteriomorpha, Fg 4.21
larval mortality estimates, 53
larval recruitment, 712
larval retention, 316
larval settlement
active selection, 55
Adalaria proxima, 577
cues, 54
passive deposition, 55
larval shell
Opisthobranchia, 591
Scaphopoda, 436, 437
larval stages, 25
Gastropoda, 591
larviparity
Heterodonta, 303
Mactridae, 338
Mesodesmatidae, 339
Pholadidae, 362
Teredinidae, 362, 374
Lasaea
dimorphic spermatozoa, 316
distribution, 318
habitat, 318
Lasaea australis
development, 316
shell structure, 317
Lasaea rubra
habitat, 318
lasidium larva, Muteloidea, 296
l'Astrolabe, 7, 162, 499, 568, 919, 1038
lateral line system
Coleidea, 468
lateral teeth, 14
Laternula, 401, 404, 410–412
habitat, 402
sculpture, 398
shadow reflex, 219
sub-tentacles, 213
Laternula anatina, habitat, 402
ligament, 411
Laternula anserifera, 407, 412
distribution, 404, 412
ligament, 411
Laternula boschansina
lithodesma, 407
Laternula constricta
hinge plate, Fg 4.6
shell form, Fg 4.2
Laternula creccina, 404
distribution, 404, 412
sculpture, Fg 9.10
shell, Fg 9.10
Laternula elliptica, 407, 412
distribution, 404, 412
ligament, 411
Laternula limicola
acrosome structure, 401
Laternula recta
distribution, 404
shell form, 199
Laternula rostrata
habitat, 402
Laternula tasmanica, 404
habitat, 402
Laternula truncata, 397, 404, 412
distribution, 404
eyes, 213
fourth pallial aperture, 412
habitat, 402
internal morphology, Fg 9.10
lithodesma, Fg 9.10, 407
pallial eyes, Fg 4.17
sensory structures, Fg 9.3
shell thickness, 412
siphons, Fg 9.10
Laternulidae, Fg 4.2, Fg 4.6, Fg 4.17, Fg 9.3, Fg 9.10
family treatment, 410
Latiaxis, shell, 824
Latirus polygonus
operculum, Fg 15.163
shell, Fg 15.163
Latirus spiceri, Pl 28
Latisageceras, Triassic, 97
Latouchella, Cambrian, 89
Latouchella accordionata
Cambrian, Fg 1.97
Latouchella merino
Cambrian, Fg 1.97
Latouchella penecyrano
Cambrian, Fg 1.97
Laubierina, 793, 798, 799
osphradium, 799
protandry, 798
protoconch, 798
radula, 798
shell, 798
Laubierina peregrinator, 798
Laubierinidae, Fg 15.139, Tb 15.1, 792, 793
family treatment, 798
osphradium, 798
Laura Basin, Fg 1.95
Lavenachiton, 177
Lavenachiton clifftonensis, Fg 3.29
Le Géographe, 6, 236, 568, 919, 1038
Le Naturaliste, 6, 568, 919
Le Zélé, 7, 1038
Leachia, 540
Leachia cf. pacificus
cartilaginous stripes, Fg 13.28
external appearance, Fg 13.28
Leachia pacifica, 540
Leander, 514
leaping
Cardioidea, 13, 220
Neotrigonia margaritacea, 293
Strombidae, 13, 574
Trigoniidae, 220
learning
Coleoidea, 475
Gastropoda, 577
models, *Octopus*, Fg 11.28
Octopoda, Fg 11.28
Lecanospira
Ordovician, 93
Lecithites, Cretaceous, 99
Lecithophorus, 995
lecithotrophic larvae, 22, 23, 52
Opisthobranchia, 934
lecithotrophy, 53
Bivalvia, 217
Gastropoda, 592
Opisthobranchia, 936
Leconychia, Tb 1.6
Leda, 236
Ledella, diversity, 239
Lediidae, 239
Leeuwinian Region
non-marine molluscs, 81
Legrand, William, 10, 1038
Lehmannia
host of *Davainea proglottina*, 68
host of *Muellerius capillaris*, 68
Lehmannia flava
external appearance, Fg 17.59
Lehmannia nyctelia
external appearance, Fg 17.59
radula, Fg 17.59
Lehmannia nyctelius
reproductive system, Fg 17.59
Leichardt, Ludwig, 8
Leichhardtia, shell, 65
Leichhardtian fluvifaunula
freshwater molluscs, 81
Leichhardtian Province, Fg 1.89
Leiomya, hinge teeth, 424
Leionucula quadrata
Cretaceous, Fg 1.100
Leiopteria, Devonian, Tb 1.6
Leiopyrga
distribution, 689
as fossils, 690
Tertiary, 101
Leiosolenus
and coral boring, 253
Leminda, 1008
Leminda millecra, 1009
length at maturity
Enoplateuthinae, 521
Pyroteuthinae, 521
Lentidiinae, 366
Lentigodentalium, 439
Lentigodentalium sp.
shell, Fg 10.13
Lenwebbia protoscribiculata
apical shell sculpture, Fg 17.55
shell sculpture, Fg 17.55
Lepas, 48, 1017
as prey of *Fiona*, 938
Lepetella, Fg 15.50, 658
brooding, 654
protoconch, Fg 15.47
Lepetella tubicola, Fg 15.50
external appearance, Fg 15.46
Lepetellidae, Fg 15.45, Fg 15.47, Fg 15.48, Fg 15.50, Tb 15.1, 658
family treatment, 658
Lepetelloidea, Tb 15.1, 664
affinities, 664
characters, 655
description, 656
distribution, 654
fertilisation, 631
relationships, 610
Lepetidae, Fg 15.34, Fg 15.38, Tb 15.1, 640, 641, 646
characters, 649
deep-sea habitat, 648
family treatment, 649
relationships, 649
Lepetinae, 641
Lepetodrilidae, penis, 632
Lepetodrilus, fertilisation, 631
Lepetopsina, 641, 646
characters, 648
deep-sea habitat, 648
Lepetopsis
in Palaeozoic, 645
Lepidocardia
distribution, 360
habitat, 360
periostacum, 360
Lepidochitona, 173
hermaphroditism, 20
Lepidochitona berryana
egg hulls, Fg 3.22
Lepidochitona caverna, 172, 173
egg hulls, Fg 3.22
Lepidochitona cinerea, 165, 175
aesthete structure, Fg 3.19
lifespan, 174
ovary, Fg 3.21
radula, Fg 3.10
Lepidochitona corrugata, 173
Lepidochitona dentiens
egg hulls, Fg 3.22
Lepidochitona fernaldi, 172, 173
Lepidochitona monterosatoi
nervous system, Fg 1.16, Fg 3.16
Lepidochitona thomasi, 173
Lepidochitonidae, Fg 1.16, 180
Lepidochitoninae, 182
Lepidomeniidae, Fg 2.8, 149
family treatment, 153
Lepidopleuridae, Fg 3.16, Fg 3.19, Fg 3.21, Fg 3.24, Fg 3.31, Pl 9, 161, 178
aesthete structure, Fg 3.19
family treatment, 178
heart structure, 168
larval development, Fg 3.24
ovary, Fg 3.21
Lepidopleurina, 178
Lepidopleurinae, 178
Lepidopleurus, 178
Lepidoteuthidae, Fg 11.10, Fg 13.16, 526
family treatment, 526
Lepidoteuthis grimaldii, 49, 526
dermal cushions, Fg 13.16
external appearance, Fg 11.10, Fg 13.16
fin shape, Fg 11.10
radula, Fg 13.16, 526
Lepidozona, 182
Lepoderma, 151
Lepoderma chiastos, Fg 2.5
abundance, 149, 151
depth range, 151
external features, Fg 2.5
spicules, 150
Leporycpraera, 780
Lepsiella, 822, 823
as fossils, 824
Lepsiella vinosa, 823
imposex, 76
Leptastraea, 938
Leptaxinus, 314
Leptellidae, Fg 15.46
Leptocheilus, 493
Leptochiton, 169, 175, 178
Tertiary, 179
Leptochiton (Leptochiton), 178
Leptochiton (Parachiton), 178
Leptochiton alveolus, 161, 178
Leptochiton asellus, 174
cleavage, 173
larval development, Fg 3.24
maturity, 178
spawning, 178
Leptochiton capricornicus, 178
Leptochiton fairchildi, 178
Leptochiton kerguelensis, 178
Leptochiton liratellus, 178
Leptochiton liratus, Pl 9, 178
Leptochiton litoreus, 178
Leptochiton matthewsianus, 178
Leptochiton norfolcensis, 178
Leptochiton puppis, Fg 3.31
Leptochiton vitjazi, 165
Leptoconchus
as coral predator, 823
Leptodesma, Tb 1.6
Leptodomus
Devonian, Tb 1.6
Silurian, Tb 1.6
Leptomaria, 666
Cretaceous, 99
Leptomys, 344
Leptomysis mediterranea, 514
Lepton, shell, 318
Leptonidae, 316
Leptonoidea, 316
Leptonotis
distribution, 771

- Leptopecten*, 277
byssus, 277
- Leptoplax*, 188
- Leptopoma*, 704
affinities, 704
distribution, 85, 704
reproduction, 704
- Leptopoma minus*, 704
distribution, 85
- Leptopoma perlucida*, 704
habitat, 704
morphology, Fg 15.78
operculum, Fg 15.78
shell, Fg 15.78
- Leptopoma vitreum*
radula, Fg 15.78
- Leptoptygma*, Devonian, 95
- Leptoptygma australe*
Devonian, Fg 1.98
- Leptoscapa*, as fossils, 835
- Leptoteuthis*, as fossils, 517
- Lessonian fluvifaunula
freshwater molluscs, 81
- Lessonian Province, Fg 1.89
- Lesueur, Charles-Alexandre,
Fg 1.7, 6, 161, 549, 1038
- Lesueurilla*, Ordovician, 92
- Letomola contortus*
radula, Fg 17.56
shell, Fg 17.55
- Leucilla nuttingi*, 996
- leucoblasts, Scaphopoda, 434
- leucocytes
Bivalvia, 210
Scaphopoda, 434
- leucophores
cephalopod behaviour, 474
Cephalopoda, 454
- Leucophysema*, 956
- Leucosyrinx queenslandica*
shell, Fg 15.174
- Leucotina*, 944
distribution, 869
shell, 869
- Leucotina concinna*
shell, Fg 15.187
- Leutzenia*, diversity, 817
- Lhotsky, John, 8
- Liardetia scandens*
distribution, 85
- Libitinidae, 348
- licker, 639
see subradular organ
- life cycles
Camaenidae, 1051
Modulus modulus, 731
Sphaeriidae, 355
- life histories
Anomalodesmata, 402
Bivalvia, 217
Cephalopoda, 470
fertilisation and egg laying, 24
gametes production, 23
growth to maturity, 28
Heterodonta, 304
larval development, 25
metamorphosis, 28
Opisthobranchia, Fg 16.19
Palaeoheterodonta, 293
Polyplacophora, 174
Pulmonata, 1051
reproductive characteristics, 23
reproductive strategies, 29
- life history strategies
Sphaeriidae, 355
- life span,
Bivalvia, 218
Cephalopoda, 470
Coleoidea, 470
Opisthobranchia, 936
- Polyplacophora, 174
- Pulmonata, 1052
- Trochoidea, 672
- ligament, 261, 269, 314, 355, 409
Anomalodesmata, Fg 9.1, 398
Anomioidea, 280
Arcoidea, 250, 253
Arcoidea, 253
Arcticoidea, 348
Bivalvia, Fg 4.4, 195, 199
in boring bivalves, 363
Carditoidea, 322
Chamoidea, 302
Clavagelloidea, 398, 413
Corbiculoidea, 352
Crassatelloidea, 302, 325
Cuspidarioidea, 398
Cyamioidea, 302, 318
evolution, Bivalvia, Fg 4.5
function, 199
Galeommatoidea, 302, 316
Heterodonta, 301
Hiattelloidea, 370
lamellibranch, Fg 4.5
Limoida, 267
Limopsoidea, 258
Mactroidea, 302, 336
Myoida, 362
Myoidea, 302
Mytiloidea, 250
Nuculoidea, 237
Ostreina, 268
Ostreoida, 268
Palaeoheterodonta, 289
Pandoroidea, 398, 415
Pectinina, 275
Pectinoidea, 275
Pholadoidea, 372
Pholadomyoidea, 398, 406
Poromyoidea, 398
Protobranchia, Fg 4.5
Pterioidea, 250
Pterioidea, 261
Pteriomorphia, 249
Solemyoidea, 241
structure, 199
Tellinoidea, 342
terminology, 199
Thracioidea, 407
Tridacnoidea, 332
Trigonoidea, 295
Ungulinidae, Fg 8.6
Verticordioidea, 398
- ligament, secondary
Anomalodesmata, 398
- ligament types
Heterodonta, 302
Pteriomorphia, 249
- light organs
Batoteuthidae, 530
Chiroteuthidae, 533
Cycloteuthidae, 525
Enoplateuthidae, 521
Grimalditeuthidae, 538
Heteroteuthinae, 511
Histoteuthidae, 528
Mastigoteuthidae, 537
Octopoda, 545
Ommastrephidae, 532
Onychoteuthidae, 523
Polyceridae, 994
Sepiolidae, 510, 511
Taoniinae, 540
Triophinae, 994
Vampyromorpha, 542
Vampyroteuthidae, 542
- Liloa*, Fg 16.33, 955
external appearance, Fg 16.33
shell, Fg 16.33
- Liloa brevis*, 919, 955
- Lima*, 268
autotomy, pallial tentacles, 219
distribution, 268
swimming, 206, 219
Tertiary, 99
- Lima bassi*, 268
- Lima hians*, 268
ctenidium, 268
- Lima lima*, Pl 11, 267
association with sponges, 268
tentacles, Fg 4.22
- Limacia*, 993, 994
- Limacia ornata*, Fg 16.75
radula, Fg 16.75
- Limacidae, Fg 1.77, Fg 17.6,
Fg 17.7, Fg 17.15, Fg 17.58,
Fg 17.59, Tb 1.5, 1102
family treatment, 1102
host of *Angiostrongylus cantonensis*, 69
- Limacina*, 926, 981, 983
ovoviviparity, 49
shell form, 923
- Limacina bulimoides*, Fg 16.61, 982
shell, Fg 16.61
- Limacina helicina*, 982
distribution, 80, 594
- Limacina helicoides*, 591, 981, 982
- Limacina inflata*, Fg 16.61, 935,
936, 952, 981, 982
distribution, 941
embryo retention, 591
shell, Fg 16.61
spermatophore, 24
- Limacina lesueuri*, Fg 16.61
shell, Fg 16.61
- Limacina retroversa*, Fg 16.9,
Fg 16.12, 981, 982
distribution, 80, 594
as prey, Fg 16.12
- Limacina trochiformis*, 982
- Limacinidae, Fg 16.9, Fg 16.12,
Fg 16.61, 980
in bottom sediments, 980
family treatment, 981
pteropod ooze, 49
size, 980
- limacisation
pulmonate gut, 1043
Rathousioidea, 1064
- Limacoidea
description, 1101
families, 1102
- Limapontia*, 973, 974
- Limapontia depressa*, 973, 974
- Limapontiidae, Fg 16.19, Fg 16.55,
969
family treatment, 973
- Limapontiinae, characters, 973
- Limapontioida, characters, 969
- Limaria*, distribution, 268
- Limaria fragilis*, Fg 1.34, 268
external appearance, Fg 6.13
habit, 268
swimming, 267
- Limaria orientalis*
aggregations, 268
parasites, 268
- Limatula*, as fossils, 268
- Limatula strangei*, Pl 11
habit, 268
- Limax*
circadian rhythm, 57
host of *Davainea proglottina*, 68
shell encapsulation, 1051
- Limax marina*, 161
- Limax maximus*, Fg 1.77
courtship/mating, Fg 17.59, 590,
1102
external appearance, Fg 17.59
locomotory waves, 1042
- lime manufacture, 72
- Limea*, Tb 1.6, 268
Cretaceous, Tb 1.6
- limestone outcrops, Fg 1.101
importance as habitat, 107
pulmonate refugia, 1052
- Limidae, Fg 1.34, Fg 4.22, Fg 6.13,
Pl 11, 225
family treatment, 267
locomotion, 13
on reef conglomerate, 36
- Limifossor*
laboratory maintenance, 145
musculature, 146
- Limifossor talpoideus*, 146
morphology, Fg 2.2
- Limifossoridae, Fg 2.2
- Limiscala*
in Australia, 816
- Limnoperla fortunei*, habitat, 219
- Limoida, 225, 249
description, 267
- Limopsidae, Fg 6.5
family treatment, 258
- Limopsis*, 259
distribution, 259
diversity in Australia, 259
as fossils, 259
Tertiary, 99
- Limopsis erectus*, 259
- Limopsis forteradiatus*, 259
- Limopsis marionensis*, mantle
cavity, Fg 6.5
- Limopsis penelevis*, 259
- Limopsis tenisoni*, 259
shell, Fg 6.5
- Limopsoidea, 253
description, 258
families, 258
- Limoptera*, Tb 1.6
- limpets, as muricid prey, 823
- Limulatys*, 955
- Linatella caudata*
feeding, Fg 15.142
- Linnaeus, 161, 431, 452
- Linopyrga*, 867
- Linopyrga pascoei*, shell, Fg 15.186
- Linotrigonia*, Cretaceous, Tb 1.6
- Linucula*, 237
- Liocerithium*, 712
- Liococha*, 360
distribution, 360
diversity, 360
habitat, 358, 360
teeth, 356
- Liococha castrensis*, 359
- Liocranchia reinhardtii*
cartilaginous stripes, Fg 13.28
external appearance, Fg 13.28
- Liocyma*, 357
direct development, 356
distribution, 360
habitat, 360
sediment on shell, 357
- Liomisusinae, 827
- Liomphalus*, Devonian, 95
- Liomphalus northi*
Devonian, Fg 1.98
- Liotiidae, 673
- Liotiinae
in Australia, 673
characters, 673
description, 673
- Liotina*, 673
- Liotina peronii*, shell, Fg 15.55
- Lippistidae, 774
- Lirobittium*, 712
- Lironoba*
distribution, 751
- Lironoba australis*, shell, Fg 15.108

INDEX

- Lirulariinae, 679, 688
Lissarca, 259–261
 hinge teeth, 260
Lissarca notorcadensis
 mantle cavity, Fg 6.7
Lissarca rhomboidalis, 260
 distribution, 261
Lissarca rubricata, shell, Fg 6.7
Lithancylus, Cretaceous, 99
 Lithotiidae, 269
Lithoconus dennanti
 Tertiary, Fg 1.101
 lithodesma, 200
 Anomalodesmata, Fg 9.1, 200, 398
 microstructure, 398
 Pandoroidea, 415
 Thracioidea, 407
 Verticordioidea, 420
Lithophaga, 253
 digestive rhythm, 209
 as parasite of chitons, 175
 in situ, Fg 6.1
Lithophaga aristata, 186
Lithophaga spatiosa, 188
Lithophaga teres, hinge, Fg 6.1
 Lithophagellidae, 348
 Lithophagidae,
 coral reef infauna, 35
 in sea grass, 39
 Lithophaginae, 250
Litiopa, 714, 715
 habitat, 715
 shell, Fg 15.87
Litiopa melanostoma, 715
 protoconch, Fg 15.87
 Litiopidae, Fg 15.87, Tb 15.1
 affinities, 712, 714, 715, 718
 family treatment, 714
 veliger, Fg 1.60
Litogyroceras, 491
 Devonian, 491
Littoraria, 738, 739
 brooding, 25, 739
 in mangroves, 45
 parental care, 637
 polymorphism, 739
 predation by crabs, 739
Littoraria cingulata, Pl 23, 739
Littoraria luteola, 739
 shell, Fg 15.100
Littoraria philippiana
 external appearance, Fg 15.100
 paraspermatozoa, Fg 1.17
Littoraria scabra, radula, Fg 5.605
Littoraria sulculosa, 739
Littorina, 632, 739
 as columbellid prey, 829
 development, 739
 distribution, 739
 egg capsule, 590
 osphradium, 577
 sperm pouches, 632
Littorina angulifera
 spermatophore, 634
Littorina littorea, 632
 circulatory system, Fg 14.20
 excretion, 627
 reproductive system, Fg 14.28
 respiration, 625
Littorina saxatilis
 brooding, 25, 637
Littorina scabra, Fg 1.48
 brooding, 25
 metamorphosis, 591
Littorina unifasciata, Fg 1.23
 Littorinidae, Fg 1.17, Fg 1.21,
 Fg 1.23, Fg 1.48, Fg 14.20,
 Fg 14.28, Fg 15.26,
 Fg 15.100, Pl 23, Tb 15.1
 buccal pouches, 621
 characters, 738
 classification, 738
 family treatment, 738
 orientation, 577
 physiological tolerance, 739
 prostate gland, 632
 on rocky shores, 29
 veliger, Fg 1.21
Littorinides, Devonian, 95
 Littorinimorpha, 703
 Littorinoidea, Tb 15.1, 606, 808
 description, 737
 liver
 Cephalopoda, 460
 Coleoidea, 500
 liver fluke vector
Austropelea tomentosa, 1056
Lymnaea columella, 1056
Pseudosuccinea columella, 67
Livonia
 as fossils, 835
 prey, 833
Livonia mamilla
 shell, Fg 15.164
Lobantale, 443
Lobiger, 932, 963, 964
Lobiger serradifalci, 964
Lobiger souverbii, 964
Lobiger viridis, 964
 Lobigeridae, 963
 Loboconcha, 3, 438
Lobophyllum, Pl 3
 host, *Calpurnus verrucosus*, 785
 as ovulid host, 786
 locomotion, 775
 adaptations for pelagic life, 613
 Anomalodesmata, 399
 Aplacophora, 149
 Bivalvia, 204
 Carinarioida, 804
 cephalopod fin, 457
 Cephalopoda, 13, 454
 ciliary, 13, 574, 1042
 Cirrata, 457, 500
 Coleoidea, 500
 Corbiculoidea, 302
 creeping, 611
 direct wave, Fg 15.4
 galloping, 1042
 Gastropoda, Fg 5.4,
 Fgs 14.9–14.11, 574
 gliding, 532
 Gymnosomata, 13
 Heterodonta, 302
 Heteropoda, 13
 jet propulsion, 13, 451, 455
 leaping, 13, 574, 612
 looping, 1042
 lurching, 612
 methods, 13
 Neomeniomorpha, 151
 Opisthobranchia, 918, 925
 Palaeoheterodonta, 290
 pedal gland, 612
 Polyplacophora, 164
 prosobranchs, 611
 Pulmonata, Fg 17.6, 1041, 1042
 Scaphopoda, 433
 shell shape, 575
 stepping, 612
 surfing, 613
 swimming, 574
 Thecosomata, 13
 uptake of water, 574
 Veneroida, 306
 wave forms, 611
 locomotor waves, 574
 direct wave, Fg 15.4
 Haliotidae, Fg 14.9
 Helicidae, Fg 14.9
 Onchidiidae, 1042
 Pomatiasidae, Fg 14.9
 Pulmonata, 1041
 retrograde wave, Fg 15.4
 Lodder, Mary, 10
Lodderena, 673
Lodderia, 765
Lodderia lodderae, 764
 Loliginidae, Fg 1.17, Fg 11.1,
 Fg 11.4, Fg 11.8, Fg 11.10,
 Fg 11.27, Fg 13.9,
 Fgs 11.14–11.16, Pl 18,
 452, 519
 family treatment, 517
 fisheries, 74
 ink and luminescence, 51
Loligo, 452, 517
 arterial system, Fg 11.15
 central nervous system, 467
 cornea, 452
 euspermatozoa, Fg 1.17
 external appearance, Fg 11.10
 fertilisation, 469
 fin shape, Fg 11.10
 food absorption, 460, 500
 mantle muscles, 500
 oxygen uptake, 501
 oxygen usage, 463
 parasites, 471
 shell, 517
 stellate ganglia, 466
 venous system, Fg 11.16
Loligo australis, 517
Loligo bleekeri
 mass mortality, 519
 semelparity, 51
Loligo chinensis, 517
Loligo etheridgei, 517
Loligo forbesi, 517
Loligo opalescens, 519
 age at sexual maturity, 519
 captive breeding, 519
 chromatophore, Fg 11.4
 courtship, 519
 egg capsule, 519
 fishery, 476
 food preferences, 519
 life span, 519
 mass mortality, 519
 mating behaviour, 519
 prey, 519
 semelparity, 51
Loligo pealei, 517
 behaviour, 519
 captive breeding, 519
 diet, ontogenetic chnge, 519
 egg laying, 519
 mating behaviour, 519
 pairing, 517
 shell, 517
 spermatophores, 519
 velocity, 517
Loligo plei, shell, 517
Loligo roperi, shell, 517
Loligo vulgaris, 517, 519
 alimentary tract, Fg 11.14
 captive breeding, 519
 jet momentum, 517
 lateral line system, 468
Loliolopsis, 517
Loliolus, shell, 517
Loliolus noctiluca, 471, 517, 520
 age at maturity, 519
 age determination, 519
 captive breeding, 519
 external appearance, Fg 13.9
 hectocotylus, Fg 13.9
 as loliginid predator, 519
 salinity tolerance, 519
Lolliguncula, 517
 mantle muscles, Fg 11.8
Lolliguncula brevis
 captive breeding, 519
 habitat, 471
 salinity tolerance, 519
Lolliguncula panamensis
 captive breeding, 519
 Lomanotidae, Fg 16.17, Fg 16.94
 family treatment, 1007
 rhinophore, Fg 16.17
Lomanotus
 external appearance, Fg 16.94
 radula, Fg 16.94
Lomanotus genei, Fg 16.17, 1007
 rhinophores, Fg 16.17
Lomanotus stauberi, 1007
Lomanotus vermiformis, 941, 1007
 looping, 1042
Lopha, 272
 Jurassic, 97
 sculpture, 272
Lopha cristagalli, Pl 12
 shell, Fg 6.15
 Lophinae, description, 271
Lophiotoma indica
 distribution, 848
 external appearance, Fg 15.174
 shell, Fg 15.174
Lophoconcha
 Ordovician, Tb 1.6
Lophopleura, 963
Lophopleurella, 963
Lophospira,
 Devonian, 95
 Ordovician, 92
Lora trevelliiana
 prey capture, Fg 14.23
 Lord Howe Island, Fg 1.108, 78,
 83, 84, 86–88, 106, 114, 178,
 181, 187–189
 Achatinellidae, 1080
 Ancyliidae, 114
 Assimineidae, 757
Austropyrgus, 755
Batillaria australis, 722
 Bulimulidae, Fg 17.23
Cellana species, 647
 conservation, 113
Conus howelli, 854
 Diplommatinidae, 706
 diversity, 113
 endemic molluscs, 81
Epiglypta, 1106
 extinctions, 114
Fluvidona, 755
Fluviopupa, 755
 fossil record, 1058
Gabrielona, 677
Gudeoconcha, 1106
Hawaii minuscula, 1104
Hedleyoconcha, 1057
 Helicariionidae, 1102, 1106
 Hemistomia, 755
Hinea brasiliiana, 724
 Hydrobiidae, 755
Mathewsoconcha, 1106
 molluscan affinities, 1057
Monterissa, 694
Monterissa gowerensis, 701
Nerita atramentosa, 695
Palaina, 706, 1057
Palaina macgillivrayi, Fg 15.80
Placostylus, 1057
Placostylus bivaricosus, Fg 17.23
Pyrasus ebeninus, 722
Vallonia pulchella, 1084
 Zonitidae, 1104
Lorica, 183
 Tertiary, 184

- Lorica cimolia*, 183
Lorica volvox, Fg 3.36, Pl 9, 183, 184
 Loricata, 2
Loricella, 183
 Tertiary, 184
Loricella angasi, Fg 3.35, 165, 183–184
Loricella profundior, 184
Loripes lacteus
 egg capsules, 216
Lortella
 affinities, 59
 distribution, 82, 298
 endemic, 293
 in Leichhardtian fluvifauuna, 81
Lortella froggatti, 298
Lortella rugata, 298
 shell, Fg 7.9D
 Lortellinae, 59
Lottia, 651
 distribution, 651
 radula, Fg 15.34
Lottia gigantea
 homing behaviour, 577
Lottia mixta, 651
Lottia onychitis, 651
 shell, Fg 15.39
 Lottiidae, Fg 15.34, Fg 15.39, Fg 15.40, Tb 15.1, 639, 641, 646
 ecological research, 643
 family treatment, 649
 Lottiinae, 641, 649
 description, 650
 origin and dispersal, 650
 love darts
 Helicoidea, 1050
 Pulmonata, 1055
Loxonema
 Carboniferous, 95
 Devonian, 95
 Silurian, 95
Loxonema altacostatum
 Devonian, Fg 1.98
Loxonema lamellosa
 Carboniferous, Fg 1.99
Lucidestea
 distribution, 751
 operculum, 749
Lucidestea atkinsoni
 operculum, Fg 15.108
 radula, Fg 15.108
 shell, Fg 15.108
Lucilina, 187
Lucina, 310
Lucina floridana, 313
 and seagrass, 313
 Lucinidae, Fg 4.3, Fg 4.10, Fg 8.2, Fg 8.3, 309
 family treatment, 310
 on reef flat, 35
 symbiotic bacteria, 207
 Lucinoidea, Fg 8.3, Fg 8.5, Fg 8.6, 309
 description, 309
 families, 309
Lucinoma
 Cainozoic, 314
 Ludbrook, N.H., 594
Luidia, molluscan predator, 39
 luminescence
 Propeamussiidae, 278
 cephalopod ink, 51
 lung
 Athoracophoridae, 1109
 Onchidiidae, 1063
 Onchidioidea, 1063
 Otinoidea, 1062
 Pulmonata, 17, 580, 1037
 Rathousiidae, 1065
 Rathousioidea, 1064
 Smeagolidae, 1063
 Systellommatophora, 1060
 Trochomorphidae, 1105
 Veronicellidae, 1066
 lungworms, 68
Lunulicardium, Silurian, Tb 1.6
Luria, 780
Lutraria, 337
Lutraria rhynchaena, Pl 15, 339
 in middens, 72
 shell, Fg 8.22
 Lutrariinae, 337
Luzonia, hinge teeth, 424
 Lycoteuthidae, Fg 13.10, 520
 family treatment, 520
 Lycoteuthinae, genera, 520
Lycoteuthis, 520
Lycoteuthis diadema, 520
 depth range, 520
 distribution, 520
Lycoteuthis lorigera, 520
 distribution, 520
 external appearance, Fg 13.10
 radula, 520
Lymnaea, 64, 65, 586
 nervous system, Fg 17.14, 1047
 stomach, Fg 14.27
 taxonomy, 1070
Lymnaea auricularia, 67
 host of *Fasciola gigantica*, 70
Lymnaea columella
 liver fluke vector, 1056
Lymnaea peregra
 reproduction, Fg 17.17
Lymnaea stagnalis, 64, 67, 1043
 alimentary tract, Fg 17.7
 buccal function, Fg 17.9
 digestion, 1043
 digestive tract, Fg 17.31
 oxygen consumption, 1046
 reproductive system, Fg 14.32
 shadow response, 577
 Lymnaeidae, Fg 1.74, Fg 14.27, Fg 14.32, Fg 17.7, Fg 17.9, Fg 17.14, Fg 17.17, Fg 17.19, Fg 17.31, Tb 1.4
 family treatment, 1069
 as fossils, 1057
 freshwater, 62, 64
 schistosome hosts, 68
 taxonomic status, 107
 Lymnaeinae, 1071
 Lymnaeoidea
 description, 1069
 hermaphroditism, 1048
 Lymnocypridae, 328
Lyncina, 780, 784
 Lyocylinae, 772
Lyonsia, 403
 burrowing, 398, 403
 byssal gland, 399
 eyes, 401
 fourth pallial aperture, 398
 mantle gland secretion, 399
 sand bonding, 398
 sculpture, 398
Lyonsia californica
 burrowing time, 403
Lyonsia hyalina, 401
 development, 401
 as sporozoan host, 402
 as trematode host, 402
Lyonsiella, 420, 421
Lyonsiella abyssicola
 hinge, Fg 9.1
Lyonsiella formosa, 403, 420
 foot, 399
 internal morphology, Fg 9.16
 prey capture, Fg 9.5
Lyonsiella fragilis, 420
 feeding, 420
 Lyonsiidae, Fg 4.7, Fg 4.19, 399
Lyrenaeta, 835
Lyria
 distribution, 835
 as fossils, 835
 head, 833
 inhalant siphon, 833
 operculum, 833
Lyria mitraeformis
 shell, Fg 15.164
Lyrocardium, 331
Lyrodus
 habitat, 374
 larviparity, 374, 378
Lyrodus bipartitus, Fg 8.53
Lyrodus massa, Fg 8.53
Lyrodus medilobatus, Fg 8.53
Lyrodus pedicellatus, Fg 8.53
Lysiosquilla maculata, 318
Lysiosquilla scabricauda, 764
Lytocarpus philippinus, 1007
Lytomamites, Cretaceous, 99
- M**
- Macalia bruguieri*, distribution, 343
Macarene cookeana
 head-foot, Fg 15.55
Maccoyella, Tb 1.6, 99
 Cretaceous, Tb 1.6
Maccoyella barklyi, Tb 1.6
 Cretaceous, Fg 1.100
Maccoyella corbiensis, Tb 1.6
Maccoyella reflecta, Tb 1.6
Maccoyella rookwoodensis, Tb 1.6
Maccoyella subangularis, Tb 1.6
Maccoyella umbonalis, Tb 1.6
 MacGillivray, John, 7, 9, 919, 1038
Macgillivraya, larva of *Tonna*, 803
 Macleay, Alexander, 8
 Macleay, William, 8
Macluritella, Ordovician, 92
Maclurites, Ordovician, 92, 93
Macoma, 42
Macoma balthica
 internal morphology, Fg 8.28
Macoma candida, distribution, 343
 Macominae, 343
Macomona deltoidalis, 343
Macomona liliana, 343
 Macpherson, 569
 Macquarie Island, 178, 179, 184
 Aplacophora, 145
 Kerguelenella lateralis, 1069
 Martialia hyadesi, 533
 Nacella macquariensis, 647
 Ocheyoherpia, 157
 Proneomeniidae, 149, 155
 macroalgae
 grazing on rocky shores, 30
Macrocallista
 habitat, 360
 periostracum, 360
Macrocephalites, Jurassic, 97
Macrochilina, Devonian, 95
Macrociiliobranchia, 225
Macrocyclidae, 1091
Macrocystis, 278
Macrodomoceras, 491
Macroschisma, 669
Macroschisma producta
 external appearance, Fg 15.54
 shell, Fg 15.54
Macrozafra, shell, 827
Macruronos novaezelandiae
 as lycoteuthid predator, 520
Macra, 337
 as fossils, 339
 on sandy beaches, 37
Macra abbreviata, 339
 in middens, 72
 shell, Fg 8.22
Macra contraria, shell, Fg 8.22
Macra eximia, 339
 hinge, Fg 8.22
 hinge plate, Fg 4.6
 in middens, 72
Macra glauca
 internal morphology, Fg 8.21
Macra queenslandica, 337
Macra rufescens, 339
 Aboriginal resources, 305
 in middens, 72
Macra westralis, 337
 Mactridae, Fg 4.6, Fg 8.21, Fg 8.22, Pl 15, 337
 family treatment, 337
 genera, 339
 subfamilies, 337
 Mactrinae, 337
Mactrinula, 337
 Macroidea, 336
 description, 336
 mantle apertures, 204
 Mactromyidae, Fg 8.7, 309
 family treatment, 315
 maculotoxin
 Hapalochlaena maculosa, 500
Madiganella, 490
Madrella, 1009
Madrella aurantiaca, 1009
Madrella ferruginosa, Fg 16.98, 1009
 external appearance, Fg 16.98
Madrella gloriosa, 1009
Madrella granularis, 1009
Madrella sanguinea, 938, 1009
 Madrellidae, Fg 16.98, 1007
 diet, 938
 family treatment, 1009
Maenoceras, Devonian, 95
Magilus
 as predator of corals, 823
 shell, 824
 magnocellular lobes
 Coleoidea, 466
 Nautilus, 465
 Vampyroreuthidae, 543
Mainwaringia, 739
 hermaphroditism, 633
 Maizaniidae, 703
Malandena, distribution, 1106
Malea, 802, 803
Malea pomum
 distribution, 803
 mantle cavity, 803
 Malleidae, Fg 4.2, Fg 6.9, 225
 family treatment, 262
Malletia, 239
 distribution, 239
Malletia obtusata, 239
 pallial morphology, Fg 5.4
Malletiella, distribution, 239
 Malletiidae, Fg 5.4, 237, 239
 family treatment, 239
Malleus, 262–265
 eyes, 212
 foot, 263
 ontogenetic change, 263

INDEX

- Malleus albus*, 263
habitat, 263
shell, Fg 6.9
- Malleus malleus*, 262, 263
habitat, 263
- Malleus meridianus*
competitive advantage, 264
density, 264
habitat, 264
shell form, Fg 4.2, 199
- Malleus regula*, 263, 264
habit, 264
internal morphology, Fg 6.9
- Malluvium*, 771
habitat, 771
- Malluvium devotus*
shell placement, Fg 15.123
- Mamillocylichna*, 948, 949
- mammals
as pulmonate predators, 1054
- Mammilla*, 791
- Manchuroceras*, 489
- manganese, in shells, 696
- Mangelia*
veliger development, 638
- Mangeliinae, 850
- mangroves
characteristics, 44
distribution, 44
molluscs, 44
productivity, 45
- Manticoceras*, Devonian, 95
- mantle, 290, 332, 515, 545
Anomalodesmata, 398
Arcticoidea, 302
Bivalvia, Fg 4.8, 195
cephalopod gas exchange, 455
cephalopod locomotion, 455
Chamoidea, 302
Coleoidea, 500
Cyamioidea, 302
Glossoidea, 302
Heterodonta, 302, 303
Limacoidea, 1102
Myoidea, 362
Nudibranchia, 923
Oegopsida, 520
Ostrea edulis pediveliger, Fg 4.8
Ostreoida, 268
Patellogastropoda, 640
Pulmonata, 1039
Tridacnoidea, 302
Vampyromorpha, 542
Velutinoidea, 786
- mantle apertures
Pholadomyoidea, 406
- mantle appendages
Basommatophora, 1041
Systellommatophora, 1041
- mantle cavity, 376, 515, 545, 814, 1068
Amphiboloidea, 1067
ancestral vetigastropod, Fg 15.7
Anomalodesmata, Fg 9.7,
Fg 9.10, Fg 9.12, Fg 9.16,
Fg 9.17
Anomioidea, Fg 6.21, 280
Architectonicoidea, Fg 15.182,
858
Arcoidea, Fgs 6.2–6.4
Basommatophora, Fg 14.19, 1067
Bivalvia, 195, 203
Caenogastropoda, Fg 14.15,
Fg 15.7, 616
Campaniloidea, Fg 15.98,
Fg 15.99
cephalopod locomotion, 457
Cephalopoda, Fg 11.3, Fg 11.11,
453, 457, 464
Cerithioidea, Fg 15.84, Fg 15.88,
Fg 15.91, Fg 15.94
Cingulopsoidea, Fg 15.102
- Cocculiniformia, 654
Cocculinoidea, 655
Coleoidea, 500
Conoidea, 847
Cypraeoidea, Fg 15.130,
Fg 15.131
Dentaliida, 439
effects of torsion, 605
faecal removal, 621
Fissurelloidea, Fg 15.7
Gastropoda, Fg 14.15, Fg 14.16,
577
Glacidorboidea, 1075
Heterobranchia, Fg 15.182
Lepetelloidea, Fg 15.50, 658
Limopsoidea, Fgs 6.5–6.7
Lymnaeoidea, 1069
Muricoidea, Fg 14.14, Fg 15.155
Myoidea, 364
Naticoida, Fg 15.135
Nautiloidea, Fg 11.11
Neogastropoda, Fg 15.155,
Fg 15.168
Neritopsina, Fg 14.15
Nuculoidea, Fg 5.1
Octopoda, Fg 11.11
Omalogyroidea, 864
opening, terrestrial taxa, 625
Opisthobranchia, Fg 14.17, 915,
924
organisation, Fg 15.7
organs, 578
Ostreoida, Fg 6.14, Fg 6.15
Otinoidea, 1062
Patellogastropoda, Fg 14.15
Pectinoidea, Fg 6.19
Pleurotomarioidea, Fg 15.7, 665
Pterioidea, Fgs 6.8–6.10
Pulmonata, Fg 14.19, Fg 17.2,
580, 1037, 1039, 1046
Pyramidelloidea, 865
respiratory flow, 615
Rissoelloidea, 862
Rissooidea, Fg 15.108,
Fg 15.116, Fg 15.118, 745
Siphonarioidea, 1067
slugs, 1047
Smeagolidae, 1063
Solemyoidea, Fg 5.1
Stromboidea, Fg 15.121
Stylommatophora, 1079
Succineoidea, 1108
Systellommatophora, 1060
Teuthoidea, Fg 11.11
Tonnoidea, Fg 15.136, 793
Trochoidea, Fg 15.7, 672
Valvatoidea, 855
Velutinoidea, Fg 15.132
Vermetoidea, 778
Xenophoroidea, Fg 15.128
- mantle complex
Arionoidea, Fg 17.54, Fg 17.56
Charopidae, Fg 17.56
Corillidae, Fg 17.68
Polygyroidea, Fg 17.68
Punctidae, Fg 17.54
- mantle current flow
Arcoida, 204
bivalve mantle cavity, 204
Bivalvia, 207
Caenogastropoda, Fg 15.9,
Fg 15.14
Calyptraeidae, Fg 15.9, Fg 15.14
Cephalopoda, 464
Nuculoidea, 204
- mantle edge sensors, Bivalvia, 212
- mantle folds, 278
Anomalodesmata, Fg 9.2
Bivalvia, Fg 4.8, 204
development, 217
Pteriomorpha, 250
Veneroidea, 356
- mantle formation
pulmonate embryo, 1051
- mantle fusion
Anomalodesmata, 398
Crenellinae, 251
Mytilidae, 251
Pandoroidea, 398, 415
Pholadomyoidea, 398, 406
Poromyoidea, 398
Pteriomorpha, 249
Solenidae, 341
Verticordioidea, 398
- mantle glands
Chromodorididae, 938
Corambidae, 990
- mantle glands, radial
Anomalodesmata, Fg 9.2, 397,
398
Lyonsiidae, 399
Pandoroidea, 415
Parilimyidae, 399, 406
Periplomatidae, Fg 9.2, 410
Pholadomyoidea, 406
Thracioidea, 407
Verticordiidae, 420
- mantle lobes
Anomalodesmata, 398
Chamidae, 308
Cypraeidae, 782
fusion, 204
Gastrochaenidae, 367, 368
Myochamidae, 418
Mytiloidea, 250
Parilimyidae, 406
Velutinoidea, 786
- mantle margin
Bivalvia, 212
Trigoniidae, Fg 7.3
- mantle musculature
Coleoidea, 500
Loliginidae, Fg 11.8
- mantle rotation, Tridacnoidea, 306
- mantle shield
Limacidae, 1102
Milacidae, 1103
- mantle tunic
cephalopod musculature, 455
- mantle/shell demarcation,
Fg 4.10, Fg 4.11
- Manzonina*, distribution, 751
- Maoricolpus roseus*, 80, 716, 718
- Maoricrater explorata*, 649
- Maorites*, Cretaceous, 99
- Maorithyas*, 314
- Maranoana*, Cretaceous, Tb 1.6
- Maranoana etheridgei*, Tb 1.6
- Marcia*
distribution, 360
diversity, 360
habitat, 358, 360
- Mareleptopoma spinosa*
shell, Fg 15.101
- Margarites*, 631
- Margarites vorticiferus*
parental care, 637
- Margaritifera*, 262
- Margaritifera margaritifera*
life span, 218
- Margaritiferidae, 226, 296
- Margaritinae, 679, 692
description, 682
- Margaritini, 682
- marginal teeth, 14
- Marginella*, 838, 840
- Marginella johnstoni*
radula, Fg 15.167
- Marginellidae, Fg 14.7, Fg 15.167,
Fg 15.168, Pl 28, Tb 15.1
Australian fauna, 841
boring, 622
family treatment, 838
- prostate gland, 632
on sand plains, 38
- Margovula*, 784
host, 786
- Marianina*, 1003
organisation, Fg 16.1
- Marianina rosea*, Fg 16.88, 1003
external appearance, Fg 16.88
radula, Fg 16.88
- Marianinidae, Fg 16.88
family treatment, 1003
- mariculture, 72
Arcidae, 256
blue mussel, 76
Crassostrea gigas, 273
giant clams, 75
Mytilus, 253
Ostrea angasi, 271
oysters, 74
Pinctada maxima, 73
production, Tb 1.3
Saccostrea commercialis, 273
Saccostrea echinata, 273
Tridacnidae, Fg 8.18, 305, 336
- Mariella*, Cretaceous, 99
- Marikellia*, 318
shell, 318
- Marikellia solida*
shell, Fg 8.8
- Marinauris*, 667
as fossils, 669
- marine distributions, 79
Gastropoda, 593
- marine provinces, 78
- marine sediments
intertidal sand beaches, 37
subtidal sand plains, 37
- marine snow, 49
and Thecosomata, 981
- marine transgressions, 90, 91
Cambrian, 90
Carboniferous, 90
Cretaceous, 91
Devonian, 90
Jurassic, 91
Ordovician, 90
Permian, 91
Silurian, 90
Tertiary, 91
Triassic, 91
- Marinula*, 1078
genital ducts, 1078
habitat, 1078
- Marinula xanthostoma*
shell, Fg 17.37
- Marionia*, Pl 36, 1002
- Marionia blainvillea*, Fg 16.16
nervous system, Fg 16.16
- Marioniopsis* sp., Fg 16.86
external appearance, Fg 16.86
radula, Fg 16.86
- Marionopsis*, 1002
- Marisa*, 621
- Marsenina*, hermaphroditism, 789
- Marseniopsis*, 789, 790
- Marseniopsis pacifera*
radula, Fg 15.133
- marsupials
as camaenid predators, 1112
- marsupium, 25
Hyriidae, Fg 7.6, 291, 298
Sphaeriidae, 303
Unionoidea, 291, 296
Unionoidea, 292, 296
- Martesia*, 374, 375
- Martesia fragilis*
external appearance, Fg 8.48
shell, Fg 8.48

- Martesia striata*, 305, 374
distribution, 374
economic significance, 76, 305
external appearance,
Fg 8.45, Fg 8.48
internal morphology, Fg 8.45
shell, Fg 8.45, Fg 8.48
- Martesiinae, 375
- Martialia hyadesi*, distribution, 533
- Martyn, Thomas, 8
- Maryborough Basin, Fg 1.95
- Masters, George, 8, 9
- Mastigoteuthidae, Fg 13.25, 538
family treatment, 537
- Mastigoteuthis*, 537, 538
colouration, 538
prey capture, 458
- Mastigoteuthis agassizii*, 538
- Mastigoteuthis cordiformis*, 538
external appearance, Fg 13.25
funnel locking cartilage, Fg 13.25
radula, Fg 13.25, 538
size, 538
tubercles, 538
- Mastigoteuthis grimaldii*, 538
- Mastigoteuthis hjorti*, 538
- Mastonia limosa*
foot, Fg 15.149
head, Fg 15.149
internal morphology, Fg 15.149
- Mastoniaeforis* cf *chaperi*
protoconch, Fg 14.36, Fg 15.148
shell, Fg 15.148
- Matheria, 328
- Mathewsoconcha*
Lord Howe Island, 1106
- Mathilda*, 859
sensu lato, 858
- Mathilda elegantula*, 859
- Mathilda rosae*, 859
- Mathildidae*, Fg 687, Tb 15.1, 858
ectoparasites of corals, 859
family treatment, 859
relationships, 606
- Mathildona*, 859
- mating
Argonautidae, 554
Cephalopoda, 469
Loliginidae, 519
Octopodidae, 549
- mating behaviour
Acolidiidae, 934
Aplysiidae, Fg 14.39
Cephalopoda, 469
Chromodorididae, Fg 14.31
Fasciolaria, Fg 14.29
Fascioliariidae, Fg 14.29
Limacidae, Fg 17.59, 1102
Opisthobranchia, Fg 14.31,
Fg 14.39
Phestilla lugubris, 934
Phestilla minor, 934
- Matthevia*, Cambrian, 93
- Matthevia variabilis*
grazing, Fg 3.30
- Mattheviidae, Fg 3.26, 177
- Matthews, E.H., 163
- maturity
Camaenidae, 1051
Littorinidae, 739
- Maugean Region, 78
- Maurea*, 686
- Maurea benthicola*
radula, Fg 15.65
- Mauritia*, 780
- Mauritius, Achatinellidae, 1080
- Maxacteon*, 927, 932
- Maxacteon cratericulatus*, 937
- May, William Lewis, 10, 163,
196, 568
- McArthur Basin, Fg 1.95
- McCoy, Frederick, 8, 9, 101
- measurement, Opisthobranchia, 941
- mechanoreceptors
Anomalodesmata, 401
Cephalopoda, 468
Cuspidariidae, 424, 425
- Mecoliotia*, 740
- Mecynodontidae, 348
- Megabalanus*
boring by *Hiatella*, 371
- Megacardita incrassata*, 324
shell, Fg 8.12
- Megadenus*, diversity, 817
- Megadenus cantharelloides*
in host, Fg 15.154
- Megadesmidae, 405
- Megadesmus*
as fossils, 406
Permian, 97
- Megadesmus grandis*
Permian, Fg 1.99
- megalaesthete, Fgs 3.17–3.19, 18
- Polyplacophora, 172
- Megalocranchia abyssicola*
external appearance, Fg 13.28
- Megapitaria*, habitat, 360
periostracum, 360
- Megapodius freycinet*
as camaenid predator, 1112
- Megascolides australis*
protected species, 112
- Megaspira*, 86
distribution, 1088
- Megaspiridae, Fg 17.48, Tb 1.5, 86
family treatment, 1088
- Megathura crenulata*
pheromones, 635
- Megayoldia*, 240
- Meiocardia*, 352
- Melampinae, 1078
- Melampus*, 1078
habitat, 1078
reproductive system, 1078
stomach, Fg 17.37
- Melampus bidentatus*
egg masses, 25
- Melampus coffeus*,
radula, Fg 17.37
reproductive tract, Fg 17.37
- Melampus fasciatus*
jaw, Fg 17.37
shell, Fg 17.37
- Melanella*
diversity, 817
foot, 817
- Melanella schoutamica*
shell, Fg 15.154
- Melania scabra*, 727
as parasite host, 728
- Melaniidae, 727
- Melanochlamys*, Fg 16.6, Fg 16.8,
Fg 16.12, Fg 16.18, 926,
937, 952
alimentary tract, Fg 16.12
copulation, 934
haemocoel, Fg 16.8
mantle cavity, Fg 16.6
reproduction, Fg 16.18
- Melanochlamys cylindrica*,
Fg 16.4, 952
shell, Fg 16.4
- Melanoides*, Tb 1.2, 82, 729
brooding, 637
distribution, 65
- Melanoides aspirans*, Fg 1.73
- Melanoides denisoniensis*
distribution, 729
- Melanoides torulosa*, brooding, 637
- Melanoides tuberculata*, 727, 729
anatomy, Fg 15.94
distribution, 82, 729
as parasite host, 728, 729
shell, Fg 15.94
- Melanopsidae, 729
affinities, 709, 727, 730
- Melanopsinae, distribution, 727
- Melanopsis*, 632
- Melaxinaea*, 260
sculpture, 259
- Melaxinaea vitrea*
shell, Fg 6.6
- Meleagrinnella*,
Cretaceous, Tb 1.6
Jurassic, 97
- Meleagrinnella woodsi*
Cretaceous, Fg 1.100
- Melibe*, Pl 36, 925, 926, 1005, 1006
- Melibe leonina*
feeding, 584, 1006
ontogenetic change in diet, 1006
swimming, 575
- Melibe leporina*, Fg 16.17
rhinophores, Fg 16.17
- Melibe mirifica*, Fg 16.92
external appearance, Fg 16.92
- Melibe vexillifera*, Fg 16.19
egg masses, Fg 16.19
- Melina*, 265
- Mellitesteia*, 714
- Mellopegma*, Cambrian, 89
- Melo*
direct development, 835
dispersal, 592
distribution, 835
egg capsules, 25, 835
as fossils, 835
- Melo amphora*, Pl 28
egg mass, Fg 1.20
prey capture, Fg 14.23
- Melo miltonis*, Fg 1.6
- Melo umbilicatus*, shell, Fg 15.164
- Melocystis*, habitat, 1052
- Melongena*, distribution, 832
- Melongenidae, Fg 15.162, Tb 15.1,
827
family treatment, 831
- Melongeninae, 832
- Meloscapander*, 948, 949
- Meloscapander grandis*, Fg 16.4
shell, Fg 16.4
- Melosidula zonata*, Fg 1.48,
Fg 17.37
- Meluvium devotus*
radula, Fg 15.123
- Membranipora*, Pl 35, 991, 992
as food of Corambidae, 990
as prey of Doridina, 938
- Membranipora crustulenta*, 991
- Membranipora membranacea*
effect of predation, 991
- memory
Coleoidea, 466, 475
Gastropoda, 577
- Mendax trizonalis*
operculum, Fg 15.150
radula, Fg 15.150
- meningoencephaly
angiostrongylosis, 1056
- Menke, Karl Theodor, 8
- Meracomelon lloydi*
as fossil, 1058
- Mercatoria*, 184
- Mercenaria*, 303, 356, 358
burrowing, Fg 4.9
nymph, 356
- Mercenaria mercenaria*
development, 54
- Mereldia*, 730
affinities, 714
- Merelina elegans*
shell, Fg 15.108
- Merelina hians*, 741
- Merelina queenslandica*,
protoconch, Fg 15.108
- Meretricidae, 356
- Meretricinae, 356, 360
- Meretrix*, 357, 360
nymph, 356
- Meridolum*
feeding, 1054
habitat, 1052
oviparity, 1051
viviparity, 1051
- Meridolum gilberti*, Fg 1.61, 81
- Meridosinia*, 360
- Merismopteria*, Permian, 97
- Mermaid*, 7, 196, 919
- merobranchial gills, Fg 3.2, Fg 3.13
- Meropesta*, 337, 338
- Meropesta nicobarica*
shell, Fg 8.22
- meroplankton, 46
- pelagic molluscs, 51
- Merriidae, 771
- Mesalia*, 730
- Mesalia melanioides*, 730
- Mescalites*, Permian, 97
- Mesobeloceras*, Devonian, 95
- Mesocoelia*, Devonian, 95
- Mesodesmatidae, Fg 8.23, 337
convergence with Donacidae, 347
family treatment, 339
subfamilies, 340
- Mesodesmatinae, 340
- Mesogastropoda, Tb 14.1, 566,
606, 609, 610, 703
status, 567
- Mesoginella*, 841
shell, 838
- Mesohydrilla ipsvichensis*
Triassic, Fg 1.100
- Mesohydrilla*, Triassic, 97
- Mesopelex*, 662
- Mesopelex zelandica*
protoconch, Fg 15.45
shell, Fg 15.45
- Mesophora*
diversity in Australia, 811
- mesoplax
Jouannetiinae, 376
Martesiinae, 375
Pholadidae, Fg 8.45, Fg 8.47,
Fg 8.48
Xylophaginae, 376
- Mesoplodon carlhubbsi*, 538
- Mesorhytis*, as fossils, 843, 845
- Mesothuria*, 318
- Mesozoic
Anomalodesmata, 404, 405
Crassatelloidea, 326
fossil record, 97
Glossoidea, 351
Lucinoidea, 310
myoid radiation, 306
Ostreina, 268
Pleurotomarioidea, 665
Scaphopoda, 437
tellinoid radiation, 306
Thracioidea, 407
Valvatoidea, 856
Veneroidea, 307

INDEX

- Mesurethra, 1046
affinities, 1080
form of ureter, 581
metabolic rate
 prosobranchs, 625
 Pulmonata, 1047
Metaellesmeroceras, 487
Metalegoceras, Permian, 97
Metalegoceras kayi
 Permian, Fg 1.99
Metaminoidea, characters, 1007
metamorphosis
 Anomalodesmata, 401
 Fionidae, 1017
 Gastropoda, 591
 larvae, 54
 life history, 28
 Opisthobranchia, 937
 Patellogastropoda, 642
 solemyid larva, 243
 veliger, 638
metanephridia
 Polyplacophora, Fg 3.15
metaplex
 Martesiinae, 375
 Pholadidae, Fg 8.45, Fg 8.47
Metarminoidea, families, 1007
Metaruncina, 958
Metasepia, 505
Metasepia pfefferi, Pl 17, 505, 508
 distribution, 508, 509
 external appearance, Fg 13.2
 mantle, 505
 shell, Fg 13.3
Metastrongylidae, 68
Metaxia, dextral whorls, 809
Metaxia fuscoapicata
 protoconch, Fg 15.148
 shell, Fg 15.148
Metaxiinae, 810
Metazoa
 phylogenetic relationships, 1
Meteor, 568
methods of study
 Angariinae, 675
 Aplacophora, 149
 Architectonicidae, 862
 Cephalopoda, 476
 Coleoidea, 503
 malacology, 101
 Opisthobranchia, 941
 Pulmonata, 1058
 Stomatellinae, 685
 Trochoidea, 673
 Turbininae, 676
Mexichromis, 1000
Mexichromis macropus, Pl 35
Miamiiridae, 997
Michelia, Devonian, 95
Michelinoceras, 491
Michellian fluvifaunula
 freshwater molluscs, 81
micraesthete, Fgs 3.17–3.19,
 18, 170
 Polyplacophora, 172
Micrastraea, 675
Micratys, 955
Microciliobranchia, 225
Microcirce, 358
Microcosmuskura
 Dendrodoris citrina, 1000
Microdiscula, 857, 858, 864
 habitat, 858
 shell, 857
Microdiscula charopa
 external appearance, Fg 15.180
 radula, Fg 15.180
 shell, Fg 15.180
Microdonta
 in Riechian fluvifaunula, 81
Microdryas, 747
Microfragum, 331
Microgaza, 687
Microginella minutissima, 840
Microglyphis, 946
Microhedyle, 960
Microhedyle cornuta, Fg 16.42, 960
 external appearance, Fg 16.42
Microhedylidae, Fg 16.42
 family treatment, 960
Microhedylloidea, Fg 16.42
 characters, 960
Microliotia, 740
Microliotia saturnia, 740
 shell, Fg 15.101
Micromelaniidae, 752
Micromelo, 932, 945
Micromelo guamensis, 945
Micromelo undata, Fg 16.23, 945
 external appearance, Fg 16.23
 shell, Fg 16.23
Micromenia fodiens
 nervous system, Fg 2.3
Micromeris, 325
Micromphalus, Devonian, 95
microphagy, Valvatoidea, 856
Micropolia, 321
Micropolidae, 320
Microrissoidea, 862
Microstilifer
 diversity, 817
 shell, 817
Microtis, 684
 radula, Fg 15.64
Microtis heckeliana
 head-foot, Fg 15.64
Microvoluta, 843
 development, 842
 egg capsules, 842
 radula, 842
Microvoluta australis
 shell, Fg 15.170
Microvoluta marginata
 anterior gut, Fg 15.170
Microyoldia, 240
 middens, Fg 1.36
 midgut gland
 Cephalopoda, 460
 Coleoidea, 500
Midorigai, 965
migration
 Ommastrephidae, 532, 533
 Onychoteuthidae, 524
 Teuthoidea, 471
Mikadotrochus, 666
Milacidae, Fg 17.58, Fg 17.60,
 Tb 1.5, Tb 17.4, 1102
 family treatment, 1103
 Angiostrongylus cantonensis, 69
Milax
 host of *Davainea proglottina*, 68
 host of *Muellerius capillaris*, 68
Milax gagates, 1103
 distribution, 1103
 external appearance, Fg 17.60
 radula, Fg 17.60
 reproductive system, 1102
milky oyster
 fishery, 74
Milneria, incubation, 324
Mimachlamys, 277, 278
 byssus, 277
 host to *Myochama*, 418
 swimming, 277
Mimachlamys asperima, Fg 1.3,
 Pl 5, Pl 13, 275, 277
 fishery, 73, 277
 larval development, 28
 shell, Fg 6.18
Mimatys, 955
Mimelenchus, 679
mimicry
 Lamellariinae, 790
 Ovulidae, 784
Minchinia chitonis
 as chiton parasite, 175
mining, effects on molluscs, 109
Minolops, 687
Minormalletia, distribution, 239
Miocene, 336, 425, 755
 Australian pulmonates, 1058
 Cephalaspidea, 956
 Conoidea, 847
 fossil record, 101
 Nautiloidea, 493
 Pandoroidea, 415
 Patellogastropoda, 644
 Sacoglossa, 961
 Scaphopoda, 437
 Tonnoidea, 794
Miralda, 867
Mitchell, Thomas, 8
Mitchellia, Devonian, 95
Mitchellia striatula
 Devonian, Fg 1.98
Mitchellian Province, Fg 1.89
mites, as chiton symbionts, 175
Mitorthoceras, 486
Mitra, 842
 dispersal, 592
 distribution, 842
 diversity in Australia, 842
Mitra carbonaria, 6
 shell, Fg 15.169
Mitra cooki, egg laying, Fg 15.26
Mitra (Eumitra), 842
Mitra nivosa, 6
Mitra papalis, Fg 15.169
Mitrella
 distribution, 829
 feeding, 829
 habitat, 829
 shell, 827
Mitrella burchardi, 829
 feeding, 829
 prey, 829
Mitrella essingtonensis
 habitat, 829
Mitrella ligula, habitat, 829
Mitrella lincolnsensis
 external appearance, Fg 15.160
 proboscis, Fg 15.160
 shell, Fg 15.160
Mitrella puella, habitat, 829
Mitrella semiconvexa, habitat, 829
Mitreola, as fossils, 835
Mitridae, Fg 15.26, Fg 15.169,
 Tb 15.1
 family treatment, 841
 on reef flat, 35
 on reef slope, 35
Mitrinae, 841
Mitrolumninae, 850
Mnestia, 954, 955
Modiola, Jurassic, 97
Modiolaria, egg capsules, 216
Modiolaria recens, 251
Modiolinae, 250
 byssal attachment, 253
Modiolopsis, Silurian, Tb 1.6
Modiolus, 44
 gills, 251
 host to *Myochama*, 418
 mantle fusion, 251
 in seagrass, 39
 shell/body relationship, Fg 4.11
Modiolus areolatus
 hinge, Fg 6.1
 internal morphology, Fg 6.1
 shell, Fg 4.2, 198
 stomach, Fg 6.1
Modiolus demissus, 211
Modiolus metcalfei
 ctenidium, Fg 6.1
Modiolus modiolus, 253
Modiolusia, rectum, 251
Modiomorpha
 Devonian, Tb 1.6, 95
Modiomorphidae, 249, 250
Modulidae, Fg 15.96, Tb 15.1, 708
 affinities, 718, 732
 family treatment, 730
Modulus, 730
Modulus candidus, 730
Modulus carchedonius, 731
Modulus modiolus, 730, 731
 alimentary canal, Fg 14.21
 morphology, Fg 15.96
 radula, Fg 15.96
Modulus tectum, 730, 731
 shell, Fg 15.96
Moelleriinae, distribution, 673
molecular sequence data, 1060
molecular techniques, 103
Mollusca, 1
 Aboriginal resources, 72
 adaptations to life on land, 55
 Aplacophora, 2
 archetype, 1
 Aculifera, 2
 Australian parasite hosts, 66
 as bioindicators, 76
 classification, 1
 Conchifera, 3
 definition and general
 description, 1
 economic significance, 65, 76
 embryology, 22
 excretion, 16
 extinct classes, 5
 fisheries, Fg 1.79, Fg 1.80,
 Tb 1.3, 72
 general features, 1, 11
 history of discovery, 6
 hypothetical ancestor, Fg 1.2
 inland waters, 59, 61–65
 intertidal significance, 32
 on land, 55
 larvae, 12
 life histories, 23
 mangroves, 45
 marine estuarine sediments, 36
 Monoplacophora, 3
 morphology and physiology, 11
 musculature and locomotion, 13
 nervous system, 18
 origin, 1
 parasitic diseases, 65, 66, 68
 phylogeny, Fg 1.4, 1, 2
 plant pests, 71
 reproduction, 19
 respiration, 17
 on rocky shores, 29, 30
 Rostroconchia, 5
 Scaphopoda, 5
 sediments, 39, 40, 44
 segmentation, 1
 sense organs, 18
 shell, 11
 shell exports, Fg 1.85
 shell structure, 12
molluscan cross, Fg 3.23
molluscan diversity, coral reefs, 34

- molluscicides, 72
 monaulism
 Opisthobranchia, 932
Monetaria, 780
Monia, 281
 byssal notches, 280
Monia tatei, 281
Monia trigonopsis, 281
 shell, Fg 6.20
Monilea, 671
 shell, 689
Monilea callifera, Fg 1.42
 radula, Fg 15.68
 shell, Fg 15.68
Monileini, 689
 shell, 689
Monitilora, 311
Monitilora ramsayi, shell, Fg 8.3
Monodonta, 680, 683
 distribution, 683
 habitat, 672
 kidney function, 626
 reproductive system, Fg 14.28
Monodonta labio
 head-foot, Fg 15.63
 shell, Fg 15.63
Monodontinae, 679, 683
Monogamus entopodia
 on host, Fg 15.154
 monographs,
 Gastropoda, 569
 Quaternary fossils, 594
 monomyarian condition
 Pteriomorpha, 249
Monoplacophora, 1, 223, 485
 Antarctica, 3
 Cambrian, Fg 1.97, 89
 Carboniferous, 95
 characters, 3
 ect-aquasperm, 20
 in fossil record, 88
 general features, 12
 metamerism, 11
 New Zealand, 3
 Permian, 97
 reproductive structure, 20
 shell muscles, 13
Monostichoglossa, 940
 monotaxic waves, Pulmonata, 1041
 monotaxy, 13
 monotocardia, 566, 581
 excretory system, Fg 15.16
 heart, 16
Monotoidea, 275
Montacuta, 318
 dimorphic spermatozoa, 316
 male retention, 215
Montacutidae, 316
Montacutona
 and *Cerianthus*, 318
 ciliary tracts, Fg 4.12
Montacutona compacta
 protandry, 214
 sperm storage, 214
Monterissa, 694
Monterissa gowerensis
 distribution, 701
 operculum, Fg 15.76
 shell, Fg 15.76
Montfortula, 669, 671
Montfortula conoidea
 shell, Fg 15.54
Montfortula rugosa, Fg 1.23
 breeding season, 24
 habitat, 671
 radula, Fg 1.14, Fg 15.54
 moon snails, 42, 790
Mooreoceras, 491
Mopalia, 184
Mopalia hindsii, 165
Mopalia lignosa, 171
Mopalia muscosa, 184
Mopaliidae, Fg 3.7, Fg 3.37,
 Pl 9, 180
 family treatment, 184
Mopaliinae, 184
Mopsella, as ovulid host, 786
Moroteuthis, 51, 524
 colouration, 524
 commercial catch, 524
 fin, 524
 as fossils, 525
 spawning, 524
Moroteuthis ingens, beak, Fg 11.25
Moroteuthis loennbergi
 external appearance, Fg 13.14
Moroteuthis robsoni
 edibility, 524
 radula, Fg 13.14, 524
 spawning, 524
 morphology
 Calyptroidea, Fg 15.126
 Cerithioidea, Fg 15.84, Fg 15.85,
 Fg 15.95, Fg 15.96,
 Fgs 15.88–15.91
 Cingulopsoidea, Fg 15.102
 Cyclophoroidea, Fg 15.78
 and function in prosobranchs, 611
 Nautiloidea, 485
 Neogastropoda, Fg 15.168
 Neritopsina, Fg 15.73
 Anomalodesmata, Fg 9.7,
 Fg 9.10, Fg 9.12, Fg 9.14,
 Fg 9.16, Fg 9.17, 397
 Anomioidea, Fg 6.21
 Aplacophora, Fg 2.2, 145
 Arcoidea, Fgs 6.2–6.4
 Arcticoidea, Fg 8.33
 Basommatophora, Fgs 17.35–
 17.38, Fgs 17.29–17.33
 Bivalvia, Fg 4.1, 196
 Calliostoma zizyphinum, Fg 15.3
 Capuloidea, Fg 15.127
 Carditoidea, Fg 8.12
 Cephalopoda, Fg 11.3, Fg 11.8,
 Fgs 11.11–11.19, Fg 11.22,
 Fg 11.25, Fg 12.11, 453
 Chamoidea, Fg 8.1
 Coleoidea, Fg 11.17, 499
 Crassatelloidea, Fg 8.14
 Cyamioidea, Fg 8.9
 Gastropoda, Fg 14.1
 Glossoidea, Fg 8.34
 Heterodonta, 301
 Iamellibranch, Fg 4.5
 Limopsoidea, Fgs 6.5–6.7
 Lucinoidea, Fgs 8.4–8.6
 Mactroidea, Fg 8.21, Fg 8.23
 Mollusca, 11
 Muricoidea, Fg 14.14, Fg 15.155
 Myoidea, Fg 8.41, Fg 8.42
 Mytiloidea, Fg 6.1
 Nautiloidea, Fg 11.11
 Neogastropoda, Fg 15.155
 Octopoda, Fg 11.11
 Opisthobranchia, 922
 Ostreoida, Fg 6.14, Fg 6.15
 Palaeoheterodonta, 289
 Pectinoidea, Fg 6.19
 Pholadoidea, Fg 8.45, Fg 8.51
 Pinnoidea, Fg 6.12
 Polyplacophora, 163
 Protobranchia, Fg 4.5
 Ptenoglossa, Fg 15.149
 Pterioidea, Fgs 6.8–6.10
 Pulmonata, Fg 17.2, Fg 17.7,
 Fg 17.14, Fg 17.15, Fg 17.17,
 Fg 17.18, Fg 17.39,
 Fgs 17.9–17.12, 1039, 1041
 Scaphopoda, Fg 10.3, Fg 10.4,
 Fg 10.10, 432
 Solenioidea, Fg 8.26
 Stylommatophora, Fg 17.39,
 Fg 17.40, Fg 17.44, Fg 17.45
 Systellomatophora,
 Fgs 17.25–17.28
 Tellinoidea, Fg 8.28, Fg 8.32
 Teuthoidea, Fg 11.11
 Tridacnoidea, Fg 8.18
 Triphoroidea, Fg 15.149
 Veneroidea, Fg 8.37, Fg 8.39
 Morris, John, 8
 mortality
 Cerithiidae, 712
 Loliginidae, 519
 Sepiidae, 508
Morula, 822, 823
 diversity in Australia, 823
 shell, 823
Morula granulata
 shell, Fg 15.156
Morula marginalba, Fg 1.26, Pl 27
 aggregation, 32
 as bioindicator, 76
 growth rates, 32
 imposex, 76
 predation on rocky shores, 32
 prey preferences, 32
 radula, Fg 15.157
 spawning season, 24
Morum, 794, 837, 838
 diversity, 837, 838
 egg mass, 838
Morum grande, shell, Fg 15.166
Morum oniscus, 838
Moruminae, 837
 characters, 837
 mosaicostracum, 203
 mother of pearl, 73, 202, 569
 industry, 676
 Nuculidae, 237
 Pteriidae, 262
 mound springs, Fg 1.106
 effects of destruction, 107
 endemic fauna, 107
 importance of Hydrobiidae, 64
Mourgona, 969–970
Mourlonia
 Devonian, 95
 Permian, 97
 mucocytes, Neritidae, 697
Mucopetraliella ellerii
 as madrellid prey, 1009
 mucous sheet
 Vermetidae, 778
 Vermetoidea, 778
Mucronalis, diversity, 817
Mucropetraliella, 938
Mucrosquama, 176, 187
 mud whelks, 707
Muellerius capillaris
 economic importance, 68
Muensterella, Cretaceous, 99
Muensteroceras
 Carboniferous, 95, 97
 mulberry shell, Pl 27
Mulinia lateralis, 55
Mulinoides, 339
 multiple spawning, Coleoidea, 471
 multispiral coiling
 operculum, Fg 15.6
Munditia, 673
Munditia subquadrata, 674
 Munier-Chalmas
 hinge notation system, 200
Murchisonia,
 Devonian, 95
 Silurian, 95
Murchisonia fermioni
 Devonian, Fg 1.98
Murex, 823
 diversity in Australia, 823
 as fossils, 824
 habitat, 823
 shell, 792
Murex acanthostephes, Pl 27
Murex queenslandicus
 shell, Fg 15.156
Murexsul, Tertiary, 99
 Muricea, 819
 Muricidae, Fg 1.20, Fg 1.21,
 Fg 1.26, Fg 1.29, Fg 14.3,
 Fg 14.4, Fg 14.33, Fg 14.35,
 Fg 15.26, Fg 15.156,
 Fg 15.157, Pl 27, Tb 15.1
 boring, 15, 622
 coral predators, 34
 in estuaries, 42
 family treatment, 820
 larval development, 27
 locomotor wave form, 611, 612
 ornamentation, 614
 predation on bivalves, 43
 on reef slope, 35
 on rocky shores, 29
 shell collecting, 76, 115
 shell ornamentation, 614
 subfamilies, 822
 as venerid predators, 358
 Muricinae, 822
 Muricoidea, Tb 15.1, 703, 819, 845
 characters, 819
 description, 819
 families, 820
 paraphyly, 819
 radular reduction, 610
 Muricopsinae, 822
 Murray Basin, Fg 1.95
 Murray River gastropods
 faunal decline, 62
 muscle scars, Bivalvia, 199
 Hipponicidae, 770
 musculature, 204
 adductors, 204
 Anomalodesmata, 399
 Anomioidea, 205
 Aplacophora, 146
 body wall, 13
 burrowing, Bivalvia, Fg 4.9
 cephalopod mantle tunic, 455
 Cephalopoda, 454
 Chaetodermatidae, 150
 Chaetodermomorpha, 146, 150
 Clavagelloidea, 205
 cruciform muscle, 206
 Cyamioidea, 205
 Dreissenoida, 205
 foot and shell, Fg 1.13
 foot, *Neritina reclinata*, 697
 head-foot retraction, *Helix*,
 Fg 17.5
 Helix pomatia, 1041
 Heterodonta, 302
 locomotion, 13, 573
 Mytiloidea, 205
 pallial retractors, 206
 Pectinoidea, 205
 pedal elevators, 205
 pedal protractors, 205
 pedal retractors, 205
 Polyplacophora, Fg 3.5,
 Fg 3.6, 164
 Prochaetodermatidae, 150
 prosobranchs, 611
 Pulmonata, 1041, 1042
 Scaphopoda, 433
 siphonal retractors, 206
Musculista, gills, 251
Musculista glaberrima
 biomass, 304
Musculista senhousia
 larval settlement, 218
 life span, 218

INDEX

- Musculium*, protandry, 215
Musculus, byssal attachment, 253
Musculus pygmaeus, brooding, 251
 mussels, 249
 Aboriginal resources, 195
 annual catches, Tb 1.3
 in archaeology, 60
 as bioindicators, 60
 as muricid prey, 823
 production, Tb 1.3
Mussonula fallax
 pallial complex, Fg 17.56
Mutela, 289
 Mutelidae, 289
 muttonfish, 667
Mya, 268, 363–364
 adductor muscles, 364
 digestion, 364
 heart rate, 211
 hydraulic pressure, 364
 larval period, 363
 shell, 364
 shell growth, 364
 siphonal process extension, 364
Mya arctica, 370
Mya arenaria, 200
 deep burrowing, 363
 size, 363
Mya arenicola
 facultative anaerobiosis, 364
Mya dubia, 367
Myadora, 397, 416, 418
 distribution, 404, 419
 as fossils, 405
 habitat, 416, 418, 419
 pedal retractor muscles, 399
 shell, 418
 taxonomy, 418
Myadora alba
 shell, 418
Myadora boltoni, 418
Myadora brevis
 distribution, 419
 shell, Fg 9.14
Myadora delicata, distribution, 419
Myadora (Myadora), 404, 418
Myadora ovata, distribution, 419
Myadora pandoriformis,
 distribution, 419
Myadora perivalida, 405
Myadora striata, 418
 internal morphology, Fg 9.14
Myalina, Triassic, 97
 Myidae, Fg 8.41
 family treatment, 364
 genera, 364
Myllita, shell, 318
Myloceras, Cretaceous, 99
Myloceras auritulum
 Cretaceous, Fg 1.100
Myochama, 397, 405, 415, 416,
 418, 419
 cementation, 418
 commensalism, 416
 distribution, 404
 host species, 418
 shell, 418
Myochama anomioides, 418
 hinge, Fg 9.14
 on host bivalve, Fg 9.14
 host species, 418
 shell, Fg 9.14
Myochama australis
 euspermatozoa, 21
Myochama keppelliana, 418
 on host bivalve, Fg 9.14
Myochama strangei
 distribution, 419
Myochama tabida,
 habitat, 402
 host species, 418
Myochama tasmanica
 distribution, 418
 host species, 418
 Myochamidae, Fg 1.17, Fg 9.14
 family treatment, 416
Myodora, Tertiary, 99
 myoglobin, 16
 Polyplacophora, 167
 Myoida, 226, 306
 description, 362
 Myoidea
 description, 363
 families, 363
 superfamilies, 226, 363
Myonera, hinge, 424
Myonia
 as fossils, 405, 406
 Permian, 97
Myonia carinata, Permian, Fg 1.99
Myonia carinella, as fossils, 405
Myonia elongata, as fossils, 405
Myonia morrisi, as fossils, 405
 Myoniinae, 405
Myophorella, Cretaceous, Tb 1.6
 myophores, Gastrochaenidae, 368
 myophoric flange
 Cucullaeidae, 256
 Glycymerididae, 259
 Myophoricardiidae, as fossils, 326
 Myophoridae
 as trigoniid ancestor, 293
 Myopsida, 452
 description, 517
 myostracum, Fg 15.32
 Heterodonta, 302
Myrtea, haemoglobin, 313
Mysella
 development, 304
 dimorphic spermatozoa, 316
 distribution, 318
 shell, 318
 Mysellidae, 316
 Mysia, 361
Mysia pellucida, shell, Fg 8.39
 Mysidiellidae, 250
Mysouffa, 944
Mysterioceras, 491
Mysticoncha, 789–790
Mysticoncha wilsoni
 radula, Fg 15.133
 shell, Fg 15.133
Mytilarca, Devonian, Tb 1.6
 Mytilidae, Fg 1.13, Fg 1.79,
 Fg 4.2, Fg 4.6, Fg 4.11,
 Fg 4.21, Fg 6.1, Pl 10, 225
 catches, Fg 1.79, 45
 family treatment, 250
 juvenile movements, 251
 musculature, 14
 on reef conglomerate, 36
 on rocky shores, 29
 in seagrass, 39
 subfamilies, 250
 vertical zonation, 253
Mytilimeria nuttalli
 endosymbiont in tunicates, 402
 Mytilinae, 250
 Mytiloidea, 249
 characters, 225
 description, 250
 Mytiloidea, 249
Mytilus, 211, 224, 251, 253
 aerial respiration, 219
 aorta, 210
 eyes, 212
 gills, 251
 ligament, 251
 origins, 223
 plantigrade larva, Fg 4.21
 reproductive cycles, 251
 in seagrass, 39
 shell/body relationship, Fg 4.11
 spawning cycle, 251
 tentacles, 251
Mytilus californianus
 reproductive strategy, 218
Mytilus edulis, 223, 253
 eggs, 216
 life span, 218
 oxygen uptake, regulation, 211
 as pyramidellid host, 867
 reproduction, 218
 site of oxygen uptake, 211
Mytilus edulis planulatus, Pl 10,
 223, 253
 affinities, 253
 as bioindicator, 76, 221
 catches, Fg 1.79
 fishery, 76, 220, 221
 reproductive cycle, 251
Mytilus efflugens, 196
Mytilus galloprovincialis, 253
 larval omnivory, 53
Mytilus planulatus
 hinge plate, Fg 4.6
Myxas, 1071
- N**
- Naccula punctata*
 relationships, 646
 and seagrass, 644
 shell, Fg 15.36
Nacella, 641, 646, 647
 characters, 647
 distribution, 646
 habitat, 647
 radula, Fg 15.34
 shell, 647
Nacella concinna, 647
Nacella macquariensis, 647
 distribution, 647
 shell, Fg 15.36
Nacella polaris, stacking, 642
 Nacellidae, Fg 14.4, Fg 15.34,
 Fg 15.36, Pl 22, Tb 15.1,
 639–641
 family treatment, 646
Nacellina, Tb 15.1, 641, 645
 distribution, 646
 diversity in Australia, 646
 habitats, 646
 Nacellinae, characters, 645
 Nacelloidea, Tb 15.1, 641, 646
 Cretaceous, 645
 description, 646
 ecological research, 643
 link to Acmaeoeidea, 645
 nacre, Fg 4.7, 13, 569
 Bivalvia, 202
 Nuculidae, 237
 sheet, Fg 4.7
Nakamigawaia, 952
Nanamoria strophon
 Tertiary, Fg 1.101
Nanaphora
 diversity in Australia, 811
Nannamoria, as fossils, 835
Nanno
 endosiphuncular deposit, 486
Nannomactra, 337
Nanocochlea, 83
 affinities, 755
Nanomia
 as prey of *Cephalopyge*, 1006
Nanonavis, Cretaceous, Tb 1.6
Naramoceras, Cretaceous, 99
 narcotisation, 941, 1059
Nargunella, Tb 1.6
Nargunella comptorae
 Devonian, Fg 1.98
Naricava, family placement, 772
Naricava angasi, shell, Fg 15.124
 Naricidae, 771
Narraeolidia, 1016
 Nassariidae, Fg 1.38, Fg 15.29,
 Fg 15.161, Pl 27, Tb 15.1,
 827
 affinities, 830
 characters, 830
 escape behaviour, 612
 familial limits, 820
 family treatment, 829
 shell ornamentation, 614
 subfamilies, 830
 Nassariinae, 830
Nassarius, 54, 612, 820
 prostate gland, 632
 on sand plains, 38
 scavengers, 42
 veliger development, 638
Nassarius glans, shell, Fg 15.161
Nassarius incrassatus, veliger, 26
Nassarius obsoletus
 cue for settlement, 54
 development, 54
Nassarius papillosus, Fg 1.38
Nassarius particeps
 external appearance, Fg 15.161,
 Pl 27
Nassarius pauperatus, 42
Nassarius pullus
 operculum, Fg 15.161
 shell, Fg 15.161
Nassarius reticulatus
 chemoreception, 577
 veliger morphology, Fg 15.29
Natica, 791
 internalisation of shell, 573
 on sand plains, 38
Natica euzona, Fg 1.43
Naticarius, 791
Naticarius alapapilionis, Pl 27
Naticarius millepunctatus
 accessory boring organ, Fg 15.13
Naticarius onca, radula, Fg 15.134
 Naticidae, Fg 1.20, Fg 1.43,
 Fg 15.13, Fg 15.134,
 Fg 15.135, Pl 27, Tb 15.1,
 38, 790
 adaptations for burrowing, 613
 boring of shell, 15
 as corbulid predators, 366
 family treatment, 790
 locomotor wave form, 611
 as mesodesmatid predators, 340
 molluscan predators, 43
 as periplomatid predators, 403,
 410
 predation, 42
 prey capture, 790
 prostate gland, 632
 on reef flat, 35
 sandy sediments, 42
 as scaphopod predators, 437
 as solenoidean predators, 340
 subfamilies, 790
 as venerid predators, 358
 Naticinae, 790
 Naticoidea, Tb 15.1
 boring, 622
 description, 790

- Naticopsis*, Devonian, 95
natural history
 Anomalodesmata, 402
 Aplacophora, 148
 Bivalvia, 217
 Cephalopoda, 470
 Coleoidea, 502
 Heterodonta, 304
 Opisthobranchia, 936
 Palaeoheterodonta, 293
 Polyplacophora, 174
 Pulmonata, 1051
 Scaphopoda, 437
Nausitora,
 habitat, 374
 pallets, 378
Nausitora dunlopei, pallet, Fg 8.54
Nausitora hedleyi, pallet, Fg 8.54
Nautilida, 491
Nautilidae, Fg 11.1, Fg 11.10,
 Fg 11.17, Fg 11.19,
 Fg 11.25, Fg 12.1,
 Fgs 12.11–12.13, Pl 21, 485
 family treatment, 494
 prey capture, 458
Nautiliropa omicron
 shell, Fg 17.55
Nautiloidea (subclass), 99, 452, 485
 Australian fossil record, 489
 biogeography, 493
 Cambrian, Fg 12.9, 92
 circulatory system, 488
 classification, 485
 connecting rings, 489
 description, 485
 Devonian, Fg 1.98
 families, 493
 morphology, 485
 Ordovician diversity, 92
 Ordovician genera, Fg 12.9
 Permian, 97
 phylogeny, Fg 12.2, 487
 radiation, 491
 shell and siphuncle, 485
 stratigraphic range, 491
Nautiloidea (superfamily)
 description, 494
Nautilus, Fg 12.4, 170, 451–453,
 455, 459–464, 466–469, 471,
 485, 486, 488, 489, 493, 496,
 499, 630
 ammonium ions, 463
 central nervous system, Fg 11.19
 circulation, Fg 11.15, 461, 462
 coelom, 457
 ctenidia, 464
 digestive gland, 460
 dispersal, 592
 distribution, 495
 diurnal movement, 495
 ectosiphuncle, 486
 excretion, 463, Fg 11.17
 external appearance, Fg 11.1,
 Fg 11.10, 453
 eyes, 466
 feeding, 459, 471, 495
 fin shape, Fg 11.10
 gills, 464
 habitat, 494
 haemocyanin, 501
 jet propulsion, 455
 life span, 470
 mantle cavity, Fg 11.11, 457, 464
 oesophagus, 459
 outer yolk sac, 470
 oxygen usage, 463
 peripheral sinuses, 462
 prey capture, 458
 rearing, 470
 reproduction, 468
 shell, 451, 494
 statocyst, 467
 taxonomy, 495
 tentacles, 454
 touch, 468
 visual acuity, 467
Nautilus belauensis, 496
Nautilus hendersoni, 493
Nautilus macromphalus
 distribution, 496
 shell, 494
Nautilus peronatus, Jurassic, 97
Nautilus pompilius, Fg 12.11, 495,
 496
 colour variation, shell, Fg 12.13
 distribution, 494, 495
 shell, Fg 12.12, 494, 495
 swimming, Fg 12.1
Nautilus repertus, Fg 12.13, 495
 beak, Fg 11.25
Nautilus scrobiculatus
 distribution, 496
 shell, 494
Nautilus spirula, 504
Nautilus stenomphalus, Pl 21,
 495–496
 distribution, 494
 living specimens, 496
 shell, 496
Navanax, 937, 952
 chemoreception, 577
 as predator of *Bulla*, 957
Navanax inermis, 952
 feeding, 584
Neactaeonina, 943
 neck lobe, Trochidae, Fg 15.68
 necklace shell, 690
Necropupina, Fg 15.79
Nectoteuthis, 511
Needham's sac, 22
 Cephalopoda, 469
 Coleoidea, 501
Neilo, 239
Neilo australis, 80, 239
Neilonellidae, Fg 5.5, 239
 family treatment, 239
 introduced taxa, 80
Neitheia, Cretaceous, Tb 1.6
nematocysts
 Aeolidae, 938
 Aeolidina, 925
 defence in nudibranchs, 990
 Hancockiidae, 1004
 use in Aeolidae, 573
Nematoda, 68
 and Pectinidae, 277
 and Veronicellidae, 1067
Nematoglossa, 845
Nematolampas, 520
Nematomenia
 development, 148
 distribution, 149, 153
 external features, Fg 2.7
Nematomenia flavens
 distribution, 153
Nematomenia platypoda
 distribution, 153
Nembrotha, 994
 radula, Fg 16.76
Nembrotha cf. lineolata, Pl 37
Nembrothidae, status, 993
Nembrothinae, 993
 characters, 994
nemerteans
 as solenoidean predators, 340
 spiral cleavage, 22
 as turrid prey, 850
Nemertesia, 1007
Nemocardium, 331
 distribution, 223
Nemocardium lyratum
 shell, Fg 8.15
Nemocardium thetidis
 distribution, 331
Neocancilla papilo
 radular teeth, Fg 15.169
Neocardium lyratum
 shell sculpture, Fg 4.3
Neocrinites, Permian, 97
Neocrinites meridionalis
 Permian, Fg 1.99
Neodavisia, 321
Neodiastoma, 730
Neogastropoda, Tb 14.1, Tb 15.1,
 566, 606, 609, 610, 703
 adaptations for carnivory, 610
 affinities, 703
 autapomorphies, 819
 component taxa, 819
 description, 819
 and Neotaenioglossa, 610
 osphradium, 18, 630
 phylogeny, 819
 radiation, 819
 relationships, 566
 renal gland, 627
 status, 567
 synapomorphies, 808
 taxa, 703
Neogene
 Bithyniidae, 761
 Conidae, 854
 Personidae, 799
 Pleurotomariidae, 666
 Volutidae, 835
Neograhamites, Cretaceous, 99
Neolepton, 321
 external appearance, Fg 8.10
 shell, Fg 8.10
Neolepton antipodum, habitat, 321
Neolepton novacambrica, 321
Neoleptonidae, Fg 8.10, 318
 family treatment, 320
Neoleptopsidae, Fg 15.34
Neoleptopsis, 648
 radula, Fg 15.34
Neomenia
 Bass Strait, 154, 157
 burrowing, 151
 development, 148
 distribution, 149
 external features, Fg 2.9
 larval development, Fg 2.4
 Torres Strait, 156
Neomeniidae, Fg 2.4, Fg 2.9
 family treatment, 153
Neomenioidea, 20
Neomeniomorpha, 2
 characters, 2, 151, 152
 classification, 2
 description, 151
 morphology, Fg 2.2
Neomesogastropoda, 703
Neomiodontidae, 348
Neomorphaloidea, affinities, 694
Neomphalidae
 functional kidney, 626
Neomphalus, 616, 623, 632
 fertilisation, 631
 heart, 623
 nephridial gland, 626
 penis, 632
 suspension-feeding, 616, 623
Neophylloceras, Cretaceous, 99
Neopilina galathea, Fg 1.3
Neopycnodonte, 269
 distribution, 270
 shell, 269
Neopycnodonte cochlear, 269
Neorossia caroli, 514
Neorossia leptodons, 511
Neoschizodus, Triassic, 97
Neosilica, 341
Neosimnia, 784
Neosolen, 341
Neotaenioglossa, Tb 14.1, 703
 affinities, 703
 Australian fauna, 607
 and Neogastropoda, 610
 osphradium, 630
neoteny
 Clionidae, 989
 Galeommatoidea, 217, 306
Neotrigonia, 226, 289, 294, 295
 acrosome ultrastructure, Fg 7.5
 affinities, 292
 ancestor, 223
 burrowing, 296
 ctenidium, 295
 defensive behaviour, 220
 development, 292
 distribution, Fg 1.86, 79, 223,
 293, 296
 diversity, 293
 fertilisation, 292
 as fossil, 293, 296
 gill filament, 291
 hinge dentition, 290
 host to *Myochama*, 418
 mantle lobes, 204
 prodissococonch, 295
 shell, 295
 spermatozoa, 292
Neotrigonia bednalli
 distribution, 296
 hinge dentition, Fg 7.2
 shell, Fg 7.1
 shell collection, 76
Neotrigonia gemma, 293, 296
 burrowing, 204, 293
 distribution, 296
Neotrigonia lamarcki
 distribution, 296
Neotrigonia margaritacea, 293,
 296
 byssal gland, 293
 distribution, 296
 epibionts, 296
 excretory system, 291
 gill filament, Fg 7.4
 habitat, 293
 hinge plate, Fg 4.6
 mantle cavity, Fg 7.8
 mantle margin, Fg 7.3
 shell, Fg 7.8
Neotrigonia medipontea
 fossil, Fg 7.7
 Pliocene, Fg 7.7
Neotrigonia novaguineana, 296
 distribution, 293
Neotrigonia strangei
 distribution, 296
Neotrigonia uniophora
 distribution, 296
Nepean Island, fossil record, 1058
nephridial gland, 625
 Neomphalus, 626
 Peltospiridae, 626
 Trochoidea, 626, 672
 Viviparus, 626
nephridiopores
 Anomalodesmata, 401
 Trigoniidae, 291
nephridium, Bivalvia, 211
nephroliths
 Bivalvia, 211
 detoxification, 211
 Tridacnidae, 303
nephrostome
 Anomalodesmata, 401
Neptunea, 622

INDEX

- Neptunea antiqua*, nurse eggs, 635
Neptunidae, 827
Neptuninae, 827
Nerita
diversity, 695
flight response, 699
in mangroves, 45
morphology, Fg 15.73
protoconch, Fg 15.72
shell strength, 699
Nerita albicilla, 700
distribution, 695
paraspermatozoa, Fg 1.17
Nerita atramentosa, Fg 1.25, Pl 23, 31, 697, 700
age at maturity, 29
competition, 698
development, 697
distribution, 593, 695
egg mass, Fg 15.26, Fg 15.73
feeding, 697
growth, 29, 697
intraspecific competition, 31
life span, 697
in middens, 700
as prey of *Ozius truncatus*, 699
settlement, 697
shell, Fg 15.72
spawning, 697
veliger, Fg 15.73
Nerita balteata, distribution, 695
Nerita birmanica, zonation, 697
Nerita costata, distribution, 695
Nerita funiculata, 698
reproduction, 697, 698
sympatry, 698
Nerita granulosa, settlement, 697
Nerita grossa, distribution, 695
Nerita latissima, shell, 696
Nerita melanotranga, 700
Nerita milnesi, 700
Nerita planospira
distribution, 695
zonation, 697
Nerita plicata, 699
behaviour, 699
operculum, Fg 15.72
shell, Fg 15.72
Nerita polita
distribution, 695
in jewellery, 694
Nerita scabricosta, 698, 699
sympatry, 698
Nerita tessellata, shell, 696
Nerita textilis, 699
clustering, 697
orientation, 699
Nerita undata, distribution, 695
Nerita versicolor, shell, 696
neritic fauna, coleoid families, 502
Neritidae, Fg 1.17, Fg 1.25, Fg 15.16, Fg 15.22, Fg 15.26, Fg 15.72, Fg 15.73, Pl 23, Tb 1.4, Tb 15.1, 84, 610, 693
in brackish water, 62
family treatment, 695
freshwater, 695
human exploitation, 700
inland waters, 64
as parasite hosts, 694
pollution, 700
reef intertidal shore, 36
on rocky shores, 29
as trematode hosts, 700
Neritilia, distribution, 695
Neritimorpha, 693
Neritina
distribution, 695
diversity, 695
euspermatozoa, 697
habitat, 695
Neritina pulligera, distribution, 695
Neritina punctulata, 697
Neritina reclivita, foot
musculature, 697
Neritina sulcata, habitat, 695
Neritina variegata
distribution, 695
Neritina violacea
distribution, 695
shell, Fg 15.72
shell variation, 696
Neritina virginea, radula, Fg 15.73
Neritinae in Australia, 695
Neritodryas, distribution, 695
Neritoidea, Tb 15.1
in Australia, 694
description, 694
families, 610, 693
on land, 55
relationships, 606
respiratory flow, 616
Neritopsidae, Fg 15.71, Tb 15.1, 610, 693
family treatment, 694
Neritopsina, Tb 14.1, Tb 15.1, 605, 606, 610
affinities, 694
characters, 610
description, 693
egg capsule production, 636
eyes, 629
fertilisation, 631
in freshwater, 580
functional kidney, 626
gonoduct, 631
heart, 623
nerve ring, 628
nervous system, 628
oesophageal glands, 621
osphradium, 630
radiation, 694
respiratory flow, 616
shell muscles, 613
shell structure, 614
sperm morphology, 634
status, 567
veliger, 22
Neritopsis atlantica, 694
Neritopsis minmiensis
Cretaceous, Fg 1.100
Neritopsis radula, 694
distribution, 694
nerve ring, prosobranchs, 628
nervous system, Fg 1.16, 628, 707, 731, 959, 960
Amphiboloidea, Fg 17.29
Anomalodesmata, 401
Aplacophora, Fg 2.3, 147
Apogastropoda, 703
Architaenioglossa, 703
Architectonicoidea, 859
Basommatophora, 1047
Bivalvia, Fg 4.16, 195, 212
Bulloidea, 957
Caenogastropoda, Fg 15.17, 610
Cephalopoda, 18, 451, 465
Cocculinoidea, 656
Dentaliida, 435
Ellobioidea, 1076
Elysioidea, 966
Fissurelloidea, 669
Gadilida, 435
Gastropoda, Fg 14.13, 576
Gymnosomata, 986
Heterodonta, 303
Mollusca, 18
Muricoidea, 820
Neomeniomorpha, Fg 2.3
octopod arm, 466
Opisthobranchia, Fg 16.16, 576, 929
Oxynooidea, 962
Palaeoheterodonta, 291
Patellogastropoda, 642
Pholadomyoidea, 406
Polyplacophora, Fg 3.16, 18, 170
prosobranchs, Fg 15.17, 628
Pulmonata, Fg 17.14, Fg 17.39, 576, 1037, 1047
pulmonate embryo, 1051
Pyramidellidae, 867
range of structure, 18
Rissooidea, 746
Scaphopoda, Fg 10.11, 435
Sorbeoconcha, Fg 15.17, 703
Stylommatophora, Fg 17.39, 1047
Trochoidea, 672
Valvatoidea, 856
Velutinoidea, 786
Vetigastropoda, Fg 15.17, Fg 15.18
Nesiocypraea, 780
Nesopupa, 1084
distribution, 85
habitat, 1082
shell, 1082
Nesopupa mooreana
apertural dentition, Fg 17.42
sculpture, Fg 17.42
shell, Fg 17.42
Nesopuparia norfolkensis
shell, 1082
Nesopupinae, genera, 1084
Nesovitrea hammonis
effect of predation, 58
nestling
Arcoidea, 253
Arcticoidea, 348
Carditidae, 322
cue, Hiatellidae, 371
Hiatelloidea, 370
Limidae, 268
Myoida, 362
Petricolidae, 361
Trapeziidae, 348
Veneridae, 357
Vesicomidae, 351
neurosecretion, Pulmonata, 1048
neurosecretory cells
Scaphopoda, 435
neurotoxins, Conoidea, 847
neurotransmitters, Bivalvia, 210
neustonic molluscs, 80
neutral buoyancy
Cephalopoda, 49
Cranchiidae, 457, 500
Histiotentaculidae, 529
Nevenulora, 311
Neverita duplicatus
boring organ, Fg 15.135
New Caledonia, Gabrieloninae, 677
New Holland, 196
New Zealand
Hinea brasiliana, 724
Nerita atramentosa, 695
Trochinea, 683
trochoidean diversity, 673
Newmarracaroceras
Jurassic, 97
Newnsia, 947, 948
Newnsia antarctica, 948
Ngairia canaliculata
shell, Fg 17.55
Ngalia Basin, Fg 1.95
ngudgo
Solenioidea, 341
nidamental glands
Coleoidea, 501
Oegopsida, 520
Sepiolidae, 511
Nightingale Island
Argobuccinum pustulosum, 801
Nilsa, habitat, 772
Nipponatys, 955
Nipponolimopsis, distribution, 259
Nipponololigo, 517
shell, 517
Nipponopanacca, 405–407
Nipponscaphander, 949
Niso
radula, 817
sex reversal, 633
shell, 817
Nitiidella, 829
penis, 829
Nitor
distribution, 1106
habitat, 1052
Nitor kreffii, radula, Fg 17.63
Nitor medioximus
shell sculpture, Fg 17.3
Nitor pudibunda, shell, Fg 17.63
nitrogen excretion
Calliostoma, 626
prosobranchs, 625
role of kidney, 625
terrestrial molluscs, 56
nitrogen fixation, Teredinidae, 374
Noalda, Fg 16.2, 952
external features, Fg 16.2
Noalda exigua, Fg 16.31, 946
external appearance, Fg 16.31
shell, Fg 16.31
Noctepuna mayana
external appearance, Fg 17.20
Nodilittorina, 698, 738, 739
ecology, 739
egg capsule, Fg 15.100
Nodilittorina acutispira, 739
Nodilittorina australis, 739
Nodilittorina praeterrima, 739
Nodilittorina pyramidalis, Pl 23, 739
pallial oviduct, Fg 15.100
shell, Fg 15.100
spawning season, 24
Nodilittorina unifasciata, 739
anatomy, Fg 15.100
distribution, 593
spawning season, 24
Nododelphinula
Cretaceous, 99
fossil Angariinae, 675
Nododelphinula dracontis, 675
Noetia, 257
Bivalvia, 210
Noetiidae, Fg 6.4
family treatment, 257
Noetiinae, 257
Nomismoceras, Carboniferous, 97
non-marine molluscs
degree of endemism, 80
distribution and affinities, 80
Gastropoda, 594
nature, 106
species-group taxa, Tb 1.7
zoogeographical regions, 80
Noradonta, Ordovician, Tb 1.6
Norfolk Island, 78, 82, 86, 87, 106, 114, 178, 187, 188
Achatinellidae, 1080
conservation, 113, 114
Diplommatinidae, 706
diversity, 114
endemic molluscs, 81

- environmental degradation, 114
 extinction of molluscs, 114
Fanulena, 1106
Fermepalaina, 706
 fossil record, 1058
Hawaii minuscula, 1104
Helicarionidae, 1057, 1102, 1106
Hinea brasiliana, 724
 molluscan affinities, 1057
 native vegetation, 114
Nerita atramentosa, 695
Palmatina, 706
Postcobia, 755
Roybellia, 1106
Succinea norfolkensis, 1108
Tricollia variabilis, Fg 15.59
Zonitidae, 1104
 North West Shelf
 faunal affinities, 594
Nossis, 941
Nostoceras, Cretaceous, 99
Notacallista, habitat, 360
Notadusta, 780
Notarchidae, Fg 16.16, 975
Notarchinae, characters, 975
Notarchus, Fg 16.16, 976
 nervous system, Fg 16.16
Notarchus indicus, 977
Notarchus punctatus, 925
Notaspidea
 characters, 977
 diet, 937
 external appearance, 922
 internal anatomy, Fg 16.3
Nothofagus, 108, 110
Notoacmea, 639, 651, 652
 diversity, 651
Notoacmea alta, 651
Notoacmea conoidea, 651
Notoacmea corrodena, 651
Notoacmea flammea, 639, 651
Notoacmea mayi, 651
Notoacmea petterdi, shell, Fg 15.39
Notoacmea petteri, 651
Notobranchaea, 987
Notobranchaea inopinata, 987
Notobranchaea macdonaldi
 external appearance, Fg 16.67
Notobranchaea tetrabranchiata, 987
Notobranchaeidae, Fg 16.67, 986
 family treatment, 987
Notobryon, 1005
Notocallista, 357, 358, 360
 distribution, 360
 periostacum, 360
Notocallista disrupta, endemic, 357
Notocallista kingii, endemic, 357
Notocochlis, 791
Notocochlis gualtieriana
 shell, Fg 15.134
Notocorbula, 366
 shell, 366
Notocorbula coxi, shell, Fg 8.42
Notocorbula ephamilla
 Tertiary, Fg 1.101
Notocorbula hydropica
 abundance, 366
Notocorbula stolata, 366
Notocorbula vicaria
 abundance, 366
Notocrater, 662
 seminal groove, 663
Notocrater craticulata
 external appearance, Fg 15.46
Notocrater gracilis
 protoconch, Fg 15.47
Notocrater ponderi, brooding, 654
Notocypraea, Pl 26, 780, 783, 784
 association with sponges, 782
 as fossils, 784
 threat of shell collection, 76
Notodiaphana, Fg 16.39, 959
 radula, Fg 16.39
 shell, Fg 16.39
Notodiaphana fragilis, 959
Notodiaphanidae, Fg 16.39
 family treatment, 959
Notododarus gouldi
 adult, Fg 1.54
 larva, Fg 1.54
Notodorididae, 995
 status, 993
Notodoris, 995, 996
 distribution, 996
Notodoris citrina, 996
Notodoris gardineri, Fg 16.79
 external appearance, Fg 16.79
Pericharax heteroraphis, 996
 radula, Fg 16.79
Notodoris minor, 34
 with egg mass, Fg 1.28
Notogrammatodon, 256
Notogrammatodon cainozoicus
 Tertiary, Fg 1.101
Notohaliotis, 667
 as fossils, 669
Notolepton, 321
Notolimea, 268
Notoluponia, 784
 as fossils, 784
Notoluponia pyralata
 Tertiary, Fg 1.101
Notomenia
 characters, 156
 endemic, 149
Notomenia clavigera, 145
 external features, Fg 2.14
 spicules, 157
Notomeniidae, Fg 2.14
Notomya, 407
Notopala, 65, 706, 707
 affinities, 82
 distribution, 65, 707
 endemism, 707
Notopala essingtonensis, 65, 707
 habitat, 707
 reproduction, 707
 shell, Fg 15.81
Notopala hanleyi, 65, 707
 conservation status, 63
 extinction, 65
 in pipelines, 707
Notopala sublineata, 65, 707
 distribution, 707
 extinction, 65
Notopala wanjakalda
 fossil, 707
 Pleistocene, 707
Notopala waterhousii, 65, 707
 habitat, 707
 reproduction, 707
 shell, Fg 15.81
Notopeplum
 as fossils, 835
 Tertiary, 99, 101
Notoplax, 179, 188
 habitat, 175
Notoplax addenda, 188
Notoplax glauerti, 188
Notoplax leuconota, 188
Notoplax speciosa, 165, 188
Notorotalia, 950
Notosepia cliftonensis
 as fossils, 503
Notosetia, 691
Notosinister
 diversity in Australia, 811
Notospisula, 337
 as fossils, 339
Notospisula trigonella, 304
Notostreptites, Cretaceous, 99
Nototeredo, pallets, 378
Nototeredo edax
 pallets, Fg 8.54
 siphon, Fg 8.54
Nototodarus
 colouration, 532
 distribution, 533
 spawning migration, 533
Nototodarus gouldi, Pl 18
 distribution, 533
 external appearance, Fg 13.22
 fishery, 74, 533
 hctocotylus, Fg 13.22
Nototodarus hawaiiensis
 distribution, 533
Nototrigonia, Tb 1.6
Nototrigonia cinctuta, Tb 1.6
Nototrigonia minima, Tb 1.6
Notovola meridionalis, 277
Notovoluta
 as fossils, 835
 Tertiary, 101
 notum, Athoracophoridae, 1109
Noumea, Fg 16.10
 radular teeth, Fg 16.10
Noumea haliclona, 938
Noumea romeri, Fg 16.83
 jaw rodlets, Fg 16.83
 radula, Fg 16.83
Novaculina, 341, 346
Nozeba
 in Australia, 752
 Cretaceous, 752
 as fossils, 752
Nozeba topaziaca
 operculum, Fg 15.110
 radula, Fg 15.110
 shell, Fg 15.110
Nucella, 822
 egg capsules, 25
Nucella lapillus, 614
 development, 635
 oxygen consumption, 625
 respiration, 625
 veliger, 27
Nucellinae, 822
 nuchal cartilages
 Cephalopoda, Fg 11.3, 453
Nucinella, 244
Nucinella concentrica, 244
Nucinella maxima, 244
Nucinella serrei, 244
Nucinella viridula
 vestigial gut, 244
Nucinellidae, 225, 235
 family treatment, 244
Nucleolaria, 780
Nucula, Tb 1.6, 236, 237
 egg sac, 216
 shell/body relationship, Fg 4.10
 ventricle, 210
Nucula delphinodonta
 egg capsules, 216
Nucula hartvigiana, 951
Nucula obliqua
 hinge dentition, Fg 5.3
 shell, Fg 5.3
Nucula sulcata
 feeding, 237
 pallial morphology, Fg 5.3
Nucula superba
 hinge plate, Fg 4.6
 shell, Fg 5.3
Nuculana, 207, 239, 240
 Devonian, Tb 1.6
 as fossils, 240
 shell, Fg 5.6
Nuculana dohrni
 shell, Fg 5.6
Nuculana hoelscheri, as fossils, 240
Nuculana minuta
 mantle cavity, 240
 pallial morphology, Fg 5.6
Nuculana ramsayii
 shell, Fg 4.2, 199
Nuculanella, Triassic, 97
Nuculanidae, Fg 4.2, Fg 5.6, 239
 family treatment, 239
 genera, 239
Nuculanoidea, 225
 Australian families, 239
 description, 239
Nuculidae, Fg 4.6, Fg 4.10, Fg 5.2, Fg 5.3, 237
 family treatment, 237
 morphology, Fg 5.3
Nuculites, Tb 1.6
 Devonian, Tb 1.6
 Silurian, Tb 1.6
Nuculoida, 225, 235
 characters, 225
 description, 237
 shared features, Solemyoidea, 235
 feeding, 206
 status of *Pojetaia*, 223
 superfamilies, 225
Nuculoidea, description, 237
Nuculopsis, Tb 1.6, 237
 Carboniferous, 95
 as fossils, 239
 Silurian, Tb 1.6
 Triassic, 97
Nudibranchia, 916
 as carinariid prey, 806
 characters, 990
 diet, 938
 external features, 923
 internal anatomy, Fg 16.3
 parallelism, 941
 in seagrass, 39
 symbiotic zooxanthellae, 940
Numella, 315
Numella adamsi, shell, Fg 8.6
 nurse cells
 function, 24, 25
 Turbinellidae, 825
 nurse eggs, Fg 15.23
 Buccinidae, 827
 Caenogastropoda, 590, 635
 Columbellidae, 829
 Fascioliidae, 833
 Muricidae, 823
 Muricoidea, 820
 Nassariidae, 831
 nut shells, 237
Nuttallia nuttallii
 cruciform muscle, 345
 suspension-feeding, 345
Nuttallochiton, 172
Nuttallochiton mirandus, Fg 3.34, 182
 nymph, Psammobiidae, Fg 8.30
Nystiellinae, 814

Obrussena, 944
Obtortio, 733
 euspermatozoa, 708
 as fossils, 733
Obtortio cf. fulva, 733
Obtortionidae, 733

INDEX

- ocelli
 Glycymerididae, 259
 Limopsidae, 259
 Noetiidae, 257
 Philobryidae, 260
Ocellochiton, 183
Ocenebrinae, 822
Ocheyoherpia, 149, 157
 affinities, 149
 characters, 157
 copulatory spicules, 157
 external features, Fg 2.15
incertae sedis, 149
 spicules, copulatory, 157
 Octobranchia, 452
 octopine, Solenoidea, 340
 octopod arm, nervous system, 466
 Octopoda, Fgs 13.31–13.34, 452
 description, 545
 Octopodidae, Fg 1.17, Fg 11.1,
 Fg 11.7, Fgs 11.14–11.17,
 Fgs 11.19–11.22, Fg 11.25,
 Fg 11.27, Fg 13.35,
 Pl 19–Pl 21, 475, 550
 behaviour, Pl 20
 family treatment, 549
 fisheries, 74
 predation on molluscs, 38
 in seagrass, 39
 subfamilies, 549
 Octopodinae, 549
 Octopoteuthidae, Fg 11.6, Fg 11.9,
 Fg 11.10, Fg 13.13, 523
 family treatment, 523
Octopoteuthis, 523, 525
 external appearance, Fg 11.10
 fin shape, Fg 11.10
 gladius, 525
 photophores, Fg 11.6, 523
Octopoteuthis megaptera
 distribution, 523
Octopoteuthis rugosa, 523
Octopoteuthis sicula
 external appearance, Fg 13.13
 radula, 523
 radula 13.13, 524
Octopus, 462, 468, 469, 471, 475,
 549
 alimentary tract, 459
 arm nerve cords, 466
 attack initiation, 502
 Australian fishery, 550
 brain, 543
 brooding, Pl 19
 cardiac parameters, 462
 colour vision, 467
 courtship, 24
 ctenidial structure, Fg 11.18
 digestive enzymes, 500
 dymanic patterns, Fg 11.27
 enzymes, 459
 euspermatozoa, Fg 1.17
 eye structure, Fg 11.20
 feeding, 459
 food conversion rate, 460
 gas exchange, Fg 11.17
 home range, 471
 lateral line system, 468
 learning models, Fg 11.28
 models of learning, Fg 11.28
 as nautilid predator, 495
 oxygen uptake, 456, 465, 501
 oxygen usage, 463
 parasites, 471
 sperm storage, 469
 sperm survival, 469
 statocyst, Fg 11.21
 stellate ganglia, 466
 territoriality, 473
Octopus alpheus, eggs, 549
Octopus australis
 swimming, Fg 11.7
Octopus berrima, 550
 as cetacean prey, 550
 courtship, Pl 20
 eggs, Pl 20, 549
 hatchlings, Pl 20
 as seal prey, 550
 swimming, Pl 19
Octopus bunurong, 550
 eggs, 549
Octopus burryi, brooding, 469
Octopus caeruleus, 549
Octopus cyanea, 549
 eggs, 549
Octopus dierythraeus, eggs, 549
Octopus flindersi, external
 appearance, Fg 11.1
Octopus graptus, eggs, 549
Octopus horridus, Pl 19, 473
Octopus kaurna, 550
 burrowing, Pl 20
 eggs, 549
Octopus magnificus
 male organs, 467
 reproductive organs, Fg 11.22
 spermatophore, Fg 11.22
Octopus maorum, 550
 beak, Fg 11.25
 as cetacean prey, 550
 eggs, 549
 as seal prey, 550
Octopus marginatus, eggs, 549
Octopus mototi, eggs, 549
Octopus ornatus
 eggs, 549
 radula, Fg 13.35, 549
Octopus pallidus, 550
 as cetacean prey, 550
 eggs, 549
 external appearance, Fg 13.35
 hectocotylus, Fg 13.35
 as seal prey, 550
Octopus polyzenia, 549
 eggs, 549
Octopus pustulosus, 549
Octopus superciliosus, 499, 549,
 550
 eggs, 549
 as seal prey, 550
Octopus tenebricus, 549
Octopus tetricus, Pl 19, 550
 eggs, 549
 rock lobster predation, 549
Octopus variolatus, 549
Octopus vulgaris
 alimentary tract, Fg 11.14
 behaviour, Fg 11.27
 boring, 549
 buccal mass, Fg 11.13
 captive breeding, 470
 central nervous system,
 Fg 11.19, 467
 flamboyant display, Fg 11.27
 paralarva, Fg 11.7
 radula, Fg 11.13
 semelparity, 470
Octopus warringa, 550
 eggs, 549
 octopuses
 fisheries, 74
 molluscan predators, 43
Ocypode, predator on *Donax*, 37
Ocythoe, 552
 commensalism, 471
 eggs, 469
 in salps, 51
 sperm transfer, 469
Ocythoe tuberculata, 552
 external appearance, Fg 13.37
 hectocotylus, Fg 13.37
 radula, Fg 13.37, 552
 sexual dimorphism, Fg 13.37
Ocythoidae, Fg 13.37, 552
 family treatment, 552
 odontoblasts, Pulmonata, 1043
Odontoglaia, 926, 952
 radula, 952
Odontoglaia guamensis, Fg 16.4,
 Fg 16.10, Fg 16.31
 external appearance, Fg 16.31
 radular teeth, Fg 16.10
 shell, Fg 16.4
 odontophoral cartilages
 prosobranchs, 620
 odontophore, Fg 15.10
 Caenogastropoda, 617
 function in *Calliostoma*, 617
 Patellogastropoda, 617
 Pulmonata, 1043
Odostomia
 distribution, 867
 shell, 867
Odostomia angasi, shell, Fg 15.186
Odostomia seminuda
 feeding behaviour, 867
Odostomia unidentata
 proboscis, Fg 15.186
 odour, Zonitidae, 1104
 Oegopsida, 452
 description, 520
Oehlertia, Devonian, 95
Oenopota, 849
Oenopota levidensis, 849
Oenopota turricula, 632
 hermaphroditism, 633
 sex reversal, 633
 Oenopotinae, 850
Oepikila, Cambrian, 92
 oesophageal gizzard
 Opisthobranchia, 926
 oesophageal glands, 610
 Bathysciadiidae, 656
Calliostoma, 618
 Cocculiniformia, 654
 Neritoidea, 694
 prosobranchs, 621
 oesophageal pouches
 Seguenziidae, 693
 oesophagus
Calliostoma, 618
 prosobranchs, 618
 Trochidae, 618
Offadesma, 401, 409, 410
 as fossils, 410
Offadesma angasi, 397, 403,
 408–410
 aortas, 401
 burrow lining, 408
 burrowers, 410
 distribution, 404, 409
 external appearance, Fg 9.9
 fourth pallial aperture, 410
 gonads, 410
 habitat, 409, 410
 hinge, Fg 9.1
 mantle folds, 410
 radial mantle glands, Fg 9.2
 shell, Fg 9.9
 siphons, 410
 stomach, 410
 officer Basin, Fg 1.95
Oikopleura, 1006
 oil glands, 241
Okadaia elegans, 996
 boring, 583
Okenia, 991
 feeding, 992
 organisation, Fg 16.1
Okenia elegans, 991
Okenia pellucida, Fg 16.72, 992
 external appearance, Fg 16.72
 radula, Fg 16.72
Okenia plana, 941, 992
 Okeniidae, 991
Oldroydia, 178
Olea, 937, 973, 974
 olfactory lobe, *Nautilus*, 465
 olfactory organ, Coleoidea, 468
Olgasolaris tollmanni
 radula, Fg 15.74
 Oligocene
 Conoidea, 847
 fossil record, 101
 Nautiloidea, 493
 oligomerisation
 Conidae, 622
 radula, 620
 Turridae, 622
Oliva, 766, 836
 alimentary tract, 835
 carnivory, 42
 diversity in Australia, 837
 internalisation of shell, 573
 nervous system, 836
 tentacles, 835
Oliva australis
 distribution, 835
 external appearance, Fg 15.165
Oliva caerulea, shell, Fg 15.165
Oliva miniacea, radula, Fg 15.165
Oliva sayana, 836
Olivella, 835, 836
 nervous system, 836
 salivary glands, 835
 tentacles, 835
Olivella verreauxii, 836
 egg capsules, 837
 swimming, 836
 Olivellidae, 835
 Olivellinae, distribution, 835
 olives, 835
 Olividae, Fg 15.165, Pl 29,
 Tb 15.1, 820, 835
 burrowing, 613
 family treatment, 835
 proposed division, 835
 on sand plains, 38
 Olivinae, 835
Omalogyra, 864
 radula, Fg 15.185
Omalogyra atomus, 864
 protrandry, 864
 reproductive morphology, 865
Omalogyra liliputia
 distribution, 864
 external appearance, Fg 15.185
 shell, Fg 15.185
 Omalogyridae, Fg 15.185, Tb 15.1,
 864
 family treatment, 864
 relationships, 566, 606
 Omalogyroidea, Tb 15.1
 description, 864
Ommastrephes, 532
 external appearance, Fg 11.10
 fin shape, Fg 11.10
 light organs, 532
 spawning migration, 533
Ommastrephes bartrami, 51, 476,
 524
 distribution, 533
 external appearance, Fg 13.22
 funnel locking apparatus,
 Fg 13.22
 hectocotylus, Fg 13.22
 radula, Fg 13.22, 532
Ommastrephes gigas, 532
Ommastrephes gouldi, 532
Ommastrephes oualaniensis, 532

- Ommastrephidae, Fg 1.54, Fg 11.6,
Fg 11.10, Fg 11.24,
Fg 11.25, Fg 13.22, Pl 18,
532
as architeuthid prey, 528
family treatment, 532
fisheries, 74
subfamilies, 532
- Ommastrephinae, 532
- Omniglypta, 443
- Omniglypta anulosum, 443
shell, Fg 10.18
- Omniglypta cerina, 443
- Omniglyptidae, Fg 10.18
family treatment, 443
- omnivory, Muricoidea, 820
- Omphalotropinae
Assimineidae, 757
distribution, 757
- Omphalotropis albocarinata
radula, Fg 15.113
shell, Fg 15.113
- Onchidella, 1063
penis, 1063
- Onchidella celtica, 1063
larval shell and operculum, 1051
- Onchidella patelloides
external appearance, Fg 17.26
habitat, 1063
- Onchidiidae, Fg 17.19, Fg 17.26,
1039
family treatment, 1063
kidney, 1045
- Onchidina, 1063
- Onchidina australis
reproductive system, Fg 17.26
- Onchidioidea, 1062
description, 1063
- Onchidium, 1063
penis, 1063
- Onchidium damelii
mating season, 1063
radula, Fg 17.26
sperm ultrastructure, Fg 17.19
- Onchidium verraculatum, 1063
- Onchidorididae, Fg 16.73, 990
family treatment, 992
- Onchidoris, 992
- Onchidoris bilamellata, 934, 992
- Onchidoris depressa, 992
external appearance, Fg 16.73
radula, Fg 16.73
- Oncis, 1063
- Oncocerida, 487
Polyelasmoceridae, Fg 12.4
- Oncomelania, 756
as host to Schistosoma, 756
- Onestia, Cretaceous, Tb 1.6
- Oniscidia, 794
- Onithochiton, 187
- Onithochiton ashbyi, 187
- Onithochiton helenae, 187
- Onithochiton hirasei, 186
- Onithochiton neglectus, 171, 173,
188
brooding, 186
growth changes, 175
- Onithochiton quercinus, Fg 3.40,
172, 175
habitat, 175
homing, 175
spawning, 173, 186
- Onithochiton quercius, 187
- Onoba
development, 751
distribution, 751
reproductive system, Fg 15.108
- ontogenetic ascent, 51
- Vampyroteuthidae, 543
- ontogenetic change
Cephalopoda, Fg 11.7, 454
Cranchiidae, 502, 540
diet of *Helcion pellucidum*, 620
Octopoda, Fg 11.7
Octopodidae, Fg 11.7
Octopoteuthidae, 523
Octopus, Fg 11.7
- ontogenetic descent
Amphitretidae, 547
Architeuthidae, 528
Bolitaenidae, 546
Cephalopoda, 51
Chroteuthidae, 537
Coleoidea, 471
Cranchiidae, 540
Enopoteuthidae, 521
Histoteuthidae, 530
Octopoteuthidae, 523
- Onustus, 776
- Onuxodon margaritiferae
commensal with *Pinctada*, 262
- Onychoteuthidae, Fg 11.25,
Fg 13.14, 524
family treatment, 523
- Onychoteuthis, 524
distribution, 525
light organs, 523
schooling, 524
- Onychoteuthis banksi, 524
external appearance, Fg 13.14
- Onychoteuthis borealijaponica, 524
biology, 524
migration, 524
- Onychoteuthis rutilis, 524
- Onykia, 524
- Oochiton, 176, 183
Tertiary, 184
- Oocorys, 794, 795
- Oocorys sulcata, distribution, 795
- Oocorythidae, 795
- oocyte development
Lyonsiidae, Fg 4.19
- Opalia
distribution, 816
shell, 814
- Opalia consors, shell, Fg 15.152
- opaline gland, Anaspidea, 974
- operculum, 702, 704, 705, 707,
718, 770, 775
Amphiboloidea, Fg 17.29, 1067
Ampullarioidea, 706
Architectonicoidea, Fg 15.182,
Fg 15.183, 858
Basommatophora, 1067
Campanilloidea, Fg 15.98,
Fg 15.99, 734
Cephalaspidea, 943
Cerithioidea, Fg 15.95, Fg 15.97,
Fgs 15.85–15.87,
Fgs 15.90–15.92
Cingulopsoidea, Fgs
15.102–15.104, 741
Conoidea, 846
Cyclophoroidea, Fg 15.78
Eupulmonata, 1076
Heterobranchia, Fg 15.179,
Fgs 15.182–15.184
Muricoidea, 820
Naticoidea, Fg 15.134, 790
Neogastropoda, Fg 15.158,
Fg 15.159, Fg 15.165,
Fgs 15.161–15.163
Neritopsidae, 694
Neritopsina, Fg 15.76, Fg 15.77
non-marine gastropods, 580
Ptenoglossa, Fg 15.148,
Fg 15.150
Pulmonata, 1037
Pyramidelloidea, 865
- Rissoelloidea, Fg 15.184
- Rissooidea, Fg 15.105,
Fg 15.106, Fg 15.108,
Fg 15.116, Fg 15.118,
Fg 15.120,
Fgs 15.110–15.112, 745
Stromboidea, Fg 15.121, 766
structure, 615
Tonnoidea, Fg 15.137,
Fg 15.140, 793
Tricoliinae, 677
Triphoroidea, Fg 15.148,
Fg 15.150, 808
types of coiling, Fg 15.6
Valvatoidea, Fg 15.179, 855
Vermetoidea, 779
Xenophoroidea, Fg 15.128
- Ophicardelus, Fg 1.48, 1078
habitat, 1078
in mangroves, 45
stomach, Fg 14.27
- Ophicardelus ornatus, Fg 17.37
sperm ultrastructure, Fg 17.19
- Ophiceras, Triassic, 97
- Ophioceras, Silurian, 95
- Ophiidermella, prey capture, 850
- Ophiidermella inermis, foregut,
Fg 15.175
- Opimilda, 858, 859
- Opimilda decorata, 859
distribution, 860
shell, Fg 15.182
- Opimilda decorata aupouira, 860
- opioid peptides, Bivalvia, 210
- Opisthobranchia, Tb 14.1, Tb 16.1,
566, 607, 854
biogeography, 941
body cavities, 925
circulation, Fg 16.15, 928
classification, 942
defensive structures, Fg 16.20
description, 915
effects of detorsion, Fg 16.6
egg masses, Fg 16.19, Fg 16.52
eggs, 934
endemism, 941
evolution of body form, Fg 16.4
external appearance, Fg 16.2,
Fgs 16.21–16.108
family arrangement, Tb 16.1
feeding, Fg 16.12, 926
gizzard, Fg 16.13, Fg 16.14
gizzard plates, Fg 16.13,
Fg 16.14
grades of organisation, Fg 16.1
gut morphology, Fg 16.12
haemocoel, Fg 16.8
history of discovery, 919
jaw plates, Fg 16.11, Fg 16.82
life history, Fg 16.19
life span, 936
locomotion, 925
loss of shell, 573
methods of study, 941
morphology, Fg 16.3, 922
natural history, 936
nervous system, Fg 16.16, 628
oviparity, 25
phylogeny, 940
pseudoconch, Fg 16.64
radiation, 940
radula, Fg 16.10, Fg 16.39,
Fgs 16.72–16.83,
Fgs 16.86–16.108
reproduction, Fg 16.18, 932, 934
respiration, 928
secondary gills, 18
semelparity, 29
sense organs and nervous
system, 929, Fg 16.17
shell, Fg 16.22, Fg 16.23,
Fg 16.31, Fg 16.39, Fg 16.44,
Fg 16.56, Fg 16.61, Fg 16.62,
Fgs 16.25–16.29,
Fgs 16.33–16.36
status, 568
swimming, Fg 16.9
- Opisthomus transversus, 175
- opisthopodium
Anomalodesmata, 401
Lyonsiellinae, 420
- Opisthorchidae, 67
- Opisthorchis, Tb 1.1
- Opisthorchis viverrini, 70
- Opisthoteuthidae, Fg 13.31, Pl 19
family treatment, 545
- Opisthoteuthis, 545
locomotion, 500
spawning, 471
- Opisthoteuthis agassizii, 545
- Opisthoteuthis californiana, 545
eggs, 545
- Opisthoteuthis depressa
diet, 545
- Opisthoteuthis persephone, Pl 19,
545
depth range, 546
distribution, 546
external appearance, Fg 13.31
shell, 545
- Opisthoteuthis pluto, 545
depth range, 546
distribution, 546
shell, 545
- Opisthoteuthis vossi, eggs, 545
- Opisthotrigonia, Tb 1.6
- Opisthotrigonia nasuta
Cretaceous, Fg 1.100
- Oppletora
affinities, 84
copulatory organ, 1072
distribution, 84, 1074
- optic glands
function, Coleoidea, 470
- optic lobes
Coleoidea, 466
Nautilus, 466
- optic tentacle retraction
Athoracophoridae, Fg 17.4
Stylommatophora, Fg 17.4
- optic tentacles
Anomalodesmata, Fg 9.3
Laternulidae, Fg 9.3
- Orbicularia, 341
- Orbitestella
habitat, 858
shell, 857
- Orbitestella decorata
jaws, Fg 15.180
shell, Fg 15.180
- Orbitestellida, 607
- Orbitestellidae, Fg 15.180, 856
family treatment, 856
- Ord Basin, Fg 1.95
- Ordovician, 92
- Actinocerida, 490
- Anomalodesmata, 224, 404
- Arcoidea, 253
- bivalve evolution, 223
- Bivalvia, 306
- Crassatelloidea, 325
- Dentaliida, 437
- Dicosorida, 490
- Ellesmerocerida, 489
- Endocerida, 489
- fossil molluscs, Fg 1.98
- Heterodonta, 306, 310
- Limoida, 250, 267
- Lucinoidea, 224, 306
- marine transgressions, 90
- Modiomorphidae, 249
- Mytiloidea, 223
- Nautiloidea, Fg 12.9, 487, 493

INDEX

- Nuculidae, 239
 Oncocerida, 491
 Orthocerida, 491
 Ostreoida, 250
 Patellogastropoda, 639
 Pectinoidea, 275
 Pterioidea, 224, 250, 261
 Pteriomorpha, 249
 Rostroconchia radiation, 223
 Scaphopoda, 437
 Solemyoida, 241
 Tarphycerida, 491
 Veneroida, 306
Ordtrachia grandis
 shell, Fg 17.69, 1112
Oreocopia, Devonian, 95
 Orectospirinae, 718
 affinities, 718
Oreokera
 habitat, 1052
Oreokera cumulus, 1099
Oreokera nimbus, 1099
Oreomava otwayensis
 shell sculpture, Fg 17.3
 organ rotation
 Tridacnidae, 332
 Tridacnoidea, 332
 organe creux of Lenssen, Fg 15.73
 organogenesis
 Cephalopoda, Fg 11.23,
 Fg 11.24, 470
 Coleoidea, Fg 11.23, Fg 11.24
 Ommastrephidae, Fg 11.24, 470
 Sepia officinalis, Fg 11.23
 Teuthoidea, Fg 11.24
 organs of Will, Pinnidae, 266
 orientation, Mastigoteuthidae, 538
 origins
 Australian pulmonates, 1057
 Chamoidea, 307
 Coleoidea, 485
 Lucinoidea, 310
 Rathouisiidae, 1065
Oriocrassatella
 as fossils, 327
 Permian, 97
Oriocrassatella queenslandica
 Permian, Fg 1.99
Oriostoma, Devonian, 95
 ormers, 667
Ormoceras, 490
Ormithocerus
 as prey of veligers, 53
Ormithoteuthis, 532
 light organs, 532
Ormithoteuthis volatilis
 distribution, 533
 external appearance, Fg 13.22
 funnel locking apparatus,
 Fg 13.22
 hectocotylus, Fg 13.22
 Orthalicidae, Tb 17.4, 1061
Orthoceras, Silurian, 95
 Orthoceratoidea, 485, 487
 Orthocerida, 491
 affinities, 485
Orthochetus, Tertiary, 99
Orthocoelium streptocoelium
 parasite of *Gyraulus gilberti*, 67
 Orthogastropoda, Tb 14.1, Tb 15.1,
 639
 Caenogastropoda, 652
 Cocculinoidea, 652
 component groups, 609
 description, 652
 features, 609
 Heterobranchia, 652
 Neritopsina, 652
 status, 568
 Veligastropoda, 652
Orthomesus, 679
Orthonota
 Silurian, Tb 1.6
Orthoyoldia, 240
Orthurethra, 1046
 affinities, 1080
 Australian families, 581
 description, 1080
 diversity in Australia, 1080
 form of ureter, 581
 relationships, 1080
Oscanius hilli, ctenidia, Fg 14.17
 osmoregulation
 Basommatophora, 1045
 freshwater pulmonates, 1045
 Palaeoheterodontia, 291
 prosobranchs, 625
 Pulmonata, 1045
 Siphonariidae, 1045
 Unionoidea, 291
 osmotic pressure, Bivalvia, 211
 osphradium
 Architaenioglossa, 703
 Bivalvia, Fg 4.18, 213
 Cypracoidea, 786
 function, 932
 Gastropoda, 577
 Mollusca, 18
 Muricoidea, 820
 Nacelloidea, 642
 Neogastropoda, 18
 Neritopsina, Fg 15.74
 Opisthobranchia, 932
 Patellogastropoda, 642
 Patelloidea, 642
 prosobranchs, 630
 Sorbeoconcha, 703
 structure and classification, 630
 Tylodiniidae, 978
 Velutinoidea, 786
 Veligastropoda, 629
Ossiania, 951
Osteopelta ceticola, 663
Osteopelta mirabilis, Fg 15.50, 663
 external appearance, Fg 15.46
Osteopelta praeceps, 663
Osteopeltidae, Fg 15.46, Fg 15.48,
 Fg 15.50, Tb 15.1, 658
 family treatment, 663
Ostioma, Devonian, 95
Ostodes, radula, Fg 14.22
 Ostracoda
 as pterotracheid prey, 807
 ostracum, 569
Ostrea, 270
 distribution, 271
 Jurassic, 97
 ventricle, 210
Ostrea angasi, 270, 271
 depth range, 270
 fishery, 74, 220
 shell, Fg 6.15
Ostrea arenicola, as fossils, 271
Ostrea edulis, 54, 211
 amoebocytes, 210
 hermaphroditism, 215
 development, Fg 4.19
 eggs, 216
 larval anatomy, Fg 4.20
 larval settlement, 54
 mantle of pediveliger, Fg 4.8
 prodissococonch, Fg 4.21
 as pyramidellid host, 867
 reproductive timing, 24
Ostrea lutaria, 80, 115
Ostrea sturtiana
 as fossils, 271
Ostrea sychophilla, 196
Ostrea tuberculata, habitat, 270
Ostrea vesiculosa
 Cretaceous, Fg 1.100
 ostreid development, Fg 4.19
 Ostreidae, Fg 1.80, Fg 4.7, Fg 4.8,
 Fg 6.15, Fgs 4.19–4.21,
 Pl 11, Pl 12
 as amathinid host, 869
 family treatment, 270
 fisheries, 74
 on reef conglomerate, 36
 State fisheries, Fg 1.80
 subfamilies, 270
 veliger, Fg 1.56
Ostreina, description, 268
Ostreinae, description, 270
Ostreoida, 249
 description, 268
Otala, phototaxis, 577
Otala lactea, water loss, Tb 17.1
Otina, 1067
 affinities, 1062
 shell, 1062
Otinidae, 1047
 distribution, 1062
 kidney, 1045
Otinoidea, 1060, 1062
 description, 1062
Otoites, Jurassic, 97
Otopleura, 867
Otopleura auriscati
 shell, Fg 15.186
 Otway Basin, Fg 1.95
Ouagapia, ovoviviparity, 1091
Ovaginella, 841
 shell, 838
Ovaleda, 240
Ovatella myosotis
 genital duct, 1048
 stomach, Fg 17.37
Ovatipsa, 780
 overlap zones, endemism, 593
 oviduct gland, Rissoidae, 749
Ovinotis, 667
 oviparity, 378
 Achatinellidae, 1080
 Achatinelloidea, 1080
 Camaenoidea, 1112
 Cionelloidea, 1081
 Gastropoda, 591
 Helicidae, 1113
 Helicoidea, 1113
 Janthinidae, 814
 Limacoidea, 1102
 Megaspiridae, 1089
 Opisthobranchia, 25, 936
 Pholadidae, 362
 Pulmonata, 1037
 Rhytidoidea, 1091
 Streptaxidae, 1090
 Streptaxoidea, 1090
 Stylommatophora, 1050
 Teredinidae, 362, 374
 Teredininae, 378
 ovipositor
 Cerithioidea, 636
 Diastomatidae, 636
 ovotestis, Stylommatophora, 1049
 ovoviviparity, 1106
 Achatinoidea, 1087
 Cerithioidea, 708
 Cionelloidea, 1081
 Enidae, 1085
 Euthecosomata, 49
 Ferrussaciidae, 1087
 Gymnosomata, 989
 Helicidae, 1113
 Helicoidea, 1113
 Hydromylidae, 989
 Janthinidae, 814
 Limacoidea, 1102
 Nassariidae, 831
 non-marine taxa, 637
 Partuloidea, 1085
 Pleurodiscidae, 1084
 Pulmonata, 25, 1038, 1049
 Pupilloidea, 1082
 Rhytididae, 1091
 Rhytidoidea, 1091
 Sphaeriidae, 216
 Streptaxidae, 1090
 Streptaxoidea, 1090
 Stylommatophora, 1050
 Subulinidae, 1087
 Thiaridae, 25
 Unionoidea, 296
 Unionoidea, 296
 Viviparidae, 707
Ovula, 784, 785
Ovula ovum, 784
 distribution, 786
 external appearance, 784
 host, 786
 shell, Fg 15.131
 traditional use, 786
Ovulactaeon, 944
Ovulidae, Fg 15.131, Pl 3, Pl 6,
 Pl 26, Pl 30, Tb 15.1
 affinities of Australian fauna, 786
 cnidarian hosts, 786
 coral predators, 34
 family treatment, 784
Ovulinae, 784
 genera, 784
 Owen, Robert 1932, 452
Owenia, 937
 Oxley, John, 8
 Oxleyan Region
 non-marine molluscs, 81
Oxychilus, 1056, 1104
 external appearance, Fg 17.61
 stomach, Fg 14.27
Oxychilus alliiarius
 locomotory waves, 1042
 odour, 1104
Oxychilus cellarius, 1104
 reproductive tract, Fg 17.61
Oxychilus draparnaldi
 breeding season, 1104
 radula, Fg 17.61
 oxygen carrying capacity
 Architeuthidae, 527
 Bivalvia, 211
 Cephalopoda, 462
 Ommastrephidae, 527
 oxygen consumption
 Bivalvia, 211
 Nucella lapillus, 625
 Pulmonata, Fg 17.13, Tb 17.2,
 1046
 oxygen depletion
 tolerance in Corbulidae, 366
 oxygen uptake
 Cephalopoda, 465
 Coleoidea, 501
 Nautilidae, 464
 Nautilus, 464
 Unionoidea, 212
Oxygyrus, shell, 804
Oxygyrus keraudreni
 radula, Fg 1.14, Fg 15.145
 shell, Fg 15.145
Oxynoe, Pl 34, 963, 964
Oxynoe antillarum, 964
Oxynoe azuopunctata, 964
Oxynoe olivacea, 964
Oxynoe viridis, 964
Oxynoidae, Fg 16.45, Pl 34, Pl 37
 family treatment, 963
 relationships, 964
Oxynooidea, characters, 962
Oxytoma, Jurassic, 97
 oystercatchers
 molluscan predators, 43

oysters, 249
 Aboriginal resources, 195
 Australian catch, 220
 economic significance, 75
 fisheries, 74
 as muricid prey, 823
 production, Tb 1.3, 75
Ozium truncatus, 699

P

Pachycardiidae
 as ancestral unionoids, 294
 Pachychilidae, 729
 affinities, 709
Pachydiscus, Cretaceous, 99
Pachydiscus jacquoti, Fg 1.100
Pachykellya minima, 321
 Pacific oysters, fishery, 74
 paddy itch, 69
Paedocline doliiformis, Fg 16.12, 989
 prey capture, Fg 16.12
 paedomorphosis, 310
 Glaciorbidae, 854
 Heterobranchia, 854
 Patellogastropoda, 639
 Paladmetidae, 845
Palaeon elegans, 514
 Palaeocardiitinae, as fossils, 322
 Palaeocene, 352
 fossil record, 99
 Glossioidea, 351
 Helicoidea, 1113
 Limacoidea, 1102
 Palaeogene, 309, 778, 794, 825, 835
 Palaeoheterodonta, 225, 226
 affinities, 293
 behaviour, 293
 biogeography, phylogeny, 293
 body wall, 290
 characters, 289
 circulatory system, 290
 classification, 294
 description, 289
 distribution, 293
 ecology, 293
 economic significance, 293
 excretion, 291
 feeding and digestive system, 290
 fossil record, 294
 history of discovery, 289
 life history, 293
 locomotion, 290
 morphology and physiology, 289
 nacre, 202
 natural history, 293
 nervous system, 291
 reproduction and development, 292
 respiration, 291
 sense organs, 291
 shell microstructure, 202
Palaeoneilo, Tb 1.6
 Carboniferous, 95
 Devonian, 95
 Ordovician, Tb 1.6
 Silurian, Tb 1.6
 Palaeo-Oriental origins, 1057
Palaeoscurria
 Devonian, 95
 Palaeozoic, 645
 Palaeotaxodonta, 225, 235, 237
 shell microstructure, 202
 Palaeozoic
 Ampullarioidea, 606
 Anomalodesmata, 404

Arcticoidea, 348
 Carditoidea, 322
 Cerithioidea, 708
 Cyclophoroidea, 606
 Eupulmonata, 1076
 fossil record, 89
 Gastropoda, 594
 Heterodonta, 306
 Megadesmidae, 405
 Mollusca, 606
 Nautiloidea, 489
 Neritopsina, 606
 Ostreoida, 268
 Paragastropoda, 639
 Patellogastropoda, 645
 Pholadomyoidea, 405
 Pholadomyoidea, 406
 Pleurotomarioidea, 665
 Pterioidea, 250
 Pulmonata, 1057
 Pyramidelloidea, 865
 Scaphopoda, 437
 Sigmurethra, 1086
Palaeozygopleura
 Devonian, 95
Palaina, 706
 affinities, 1057
Palaina macgillivrayi
 shell, Fg 15.80
 Paleoloricata, 177
 Paleozoic, see Palaeozoic
Palio, 993
Paliolla, 941, 994
 pallets
 Bankiinae, Fg 8.54, 378
Kuphus, 378
 Pholadoidea, Fgs 8.51–8.54
 Teredinidae, Fgs 8.51–8.54, 362, 376
 Teredininae, 378
 pallial apertures
 Anomalodesmata, 398
 pallial configuration
 Enidae, Fg 17.45
 Mesurethra, Fg 17.39
 Orthurethra, Fg 17.39
 Partuloidea, Fg 17.45
 Pulmonata, Fg 17.39
 Sigmurethra, 1079
 Stylommatophora, Fg 17.39
 pallial eyes
 Anomiidae, 281
 Arcoidea, Fg 4.17
 Bivalvia, Fg 4.17
 Cardiidae, 330
 Cerithioidea, Fg 15.92
 Laternulidae, Fg 4.17
 Pectinidae, Fg 4.17
 Pectinoidea, 275
 Philobryidae, 260
 Potamididae, Fg 15.92
Pyrasus ebeninus, 720
 Spondylidae, 278
 Tridacnidae, Fg 4.17
 pallial gills
Lottia gigantea, 641
Patella, 579
 Patellogastropoda, 639, 640
 Patelloidea, 641
 pallial gonoducts
Nucella, 632
 Opisthobranchia, 918
Pomatias, 632
 pallial lacunae
 Cuspidariidae, 401
 Poromyidae, 401
 predation, Anomalodesmata, 401
 Verticordiidae, 401
 pallial line
 Bivalvia, Fg 4.4, 199
 Trigonioida, 295
 pallial muscle scars
 Pholadomyoidea, 406

pallial muscles
 Bivalvia, Fg 4.5
 Scaphopoda, 433
 pallial organs
 asymmetry, 615
Calliostoma, 615
 Fissurellidae, 615
 Haliotidae, 615
 Pinnidae, 265, 266
 Pleurotomariidae, 615
 prosobranchs, 615
 reduction, respiratory flow, 616
 Scissurellidae, 615
 Trochidae, 615
 Vetigastropoda, 615
 pallial retractor muscles
 Bivalvia, 206
 Cleidothaeridae, 419
 Glauconomidae, Fg 8.40
 Malleidae, 262
 Pinnidae, 266
 Poromyidae, 422
 pallial sinus
 Bivalvia, Fg 4.4
 Veneridae, Fg 4.4
 pallial tentacle
 Cornirostridae, 856
 Orbitestellidae, 856, 857
 Valvatoidea, 855
 Xylodisculidae, 858
 palliovisceral lobe, Coleoidea, 466
Palmadusta, 780
Palmatina, 706
 palp lamellae, Nuculidae, 237
 palp proboscis
 Bivalvia, Fg 4.5
 Malletidae, Fg 5.4
 Nuculanidae, Fg 5.6
 Nuculidae, Fg 5.3, 237
 Protobranchia, Fg 4.5
 Sareptidae, Fg 5.7, 240
 palps
 Heterodonta, 302
 Tellinoidea, 302
Paludina hanleyi, 706
Paludina lirata, 706
Paludomus tanschaurica
 as parasite host, 728
Palythoa, 862, 1012
Panacca, 405–407
Panacca adelaidis
 distribution, 407
Panacca mawsoni, distribution, 407
Panamicorbula, 366
 pancake octopus, Pl 19
 pancreas
 Cephalopoda, 460
 Coleoidea, 500
Pandofella, 1093
Pandofella whitei, Pl 32
Pandora, 404, 415, 416, 418
 development, 216
Pandora ceylanica, statocysts, 416
Pandora elongatus, 415
 distribution, 404
 shell, Fg 9.13
Pandora inaequalis, 401, 416
 development, Fg 9.4
 larval period, 401
Pandora patula, 416
 distribution, 404, 415–416
 shell, Fg 9.13, 416
Pandora sensu stricto, 416
 Pandoridae, Fg 9.4, Fg 9.13
 family treatment, 415
 Pandoroidea, 226
 description, 415
 habitat, 402
 origin, 415

Panenka, Tb 1.6
 Carboniferous, 95
Panomys, 370
Panope, 370
Panopea, Tb 1.6, 370, 371
 Cretaceous, Tb 1.6
 as fossils, 370
 Tertiary, 99
Panopea agnewi, 370
Panopea australis, 370, 371
 habitat, 370
 shell, Fg 8.44
Panopea generosa, 370, 371
Panopea kalimnensis, 370
Panopea ralphii, 370
Panulirus cygnus
 as solemyid predator, 244
Paphia
 distribution, 360
 diversity, 360
 habitat, 358, 360
Paphies, 37, 340
 commercial importance, 340
 on high-energy beaches, 37
 on sandy beaches, 37
 habitat, 340
Paphies angusta, as fossils, 340
Paphies australis, 340
 host to *Myochama*, 418
Paphies cuneata
 density, 340
 spawning season, 339
Paphies elongata, 339, 340
 burrowing, 340
 foot, Fg 8.23
 as fossils, 340
 prey of *Polinices conicus*, 37
 shell, Fg 8.23
 siphons, Fg 8.23
Paphies ventricosa
Paphies (Amesodesma), 339
Paphies (Mesodesma), 339
 spawning season, 339
 Paphiidae, 339
 papillary sac, Fg 15.8, 625, 626
Papuina, 1112
 Papuinidae, 86
 distribution, 1057
Paracanthoplites
 Cretaceous, 99
Paracardium, Tb 1.6
Parachiton, 178
Paraclione longicaudata,
 Fg 16.69, 989
 external appearance, Fg 16.69
Paracocculina, 656
Paracocculina cervae, 656
 cephalic tentacles, Fg 15.42
 external appearance, Fg 15.42
Paracteocina, 948, 949
Paracteocina vitjazi, Fg 16.4
 shell, Fg 16.4
Paracyclas, Tb 1.6
 Devonian, Tb 1.6, 95
 Silurian, Tb 1.6
Paradentalium, 439
Paradentalium intercalatum
 shell, Fg 10.13
Paradiala, affinities, 714
Paradisoceras, 491
Paraganitus, 960
Paraganitus ellynnae, Fg 16.42, 960
 external appearance, Fg 16.42
Paragastrioceras, Permian, 97
 Paragastropoda, 639
 characters, 3
Paragonimus westermani, 70, 757

INDEX

- Paralaoma*, 1096, 1097
Paralaoma aprica
 pallial complex, Fg 17.54
 reproductive system, Fg 17.54
Paralaoma caputspinulae
 shell, Fg 17.54
 paralarva
 Coleoidea, 502
 Octopoda, Fg 11.7
 Octopodidae, Fg 11.7
Parallelodon
 Devonian, Tb 1.6
 Permian, 97
 Silurian, Tb 1.6
 Parallelodontidae, 253
Paramegadenus, diversity, 817
 Paramphistomidae, 65, 67
 life cycle, 67
 paramphistomosis
 economic importance, 65
Paramphistomum ichikawai
Helicorbis australiensis, 67
Paramya, shell, 364
 Parancistrolepisinae, 827
Paranorites, Triassic, 97
Parantipathes, Fg 15.182
Parantipathes tenuispina
 host, *Gegania valkyrie*, 860
Parapholas, 375
Parapholas quadrizonata
 external appearance, Fg 8.48
 shell, Fg 8.48
Paraplectronoceras, 489, 493
 parapodia
 Akeridae, 975
 Elysiidae, Fg 16.48, 967
 Elysiodea, 966
 photosynthesis, 937
 Plakobranchidae, 966
 Thecosomata, 980
 parapodial lobes, Fg 16.3
Pararrhopalia, distribution, 155
 parasite research, Thiaridae, 728
 parasites, 867
 Amathinidae, 868
 Australian hosts, 66
Austroilharzia terrigalensis, 721
Austropeplea tomentosa as
 vector, 1056
 Batillariidae, as hosts, 721
Capulus, 623
 Cephalopoda, 471
Echineulima, 623
Entoconcha, 623
 eulimid on host, Fg 15.154
 Eulimidae, 15
 Eulimoidea, 817
 Gastropoda, 15
 human diseases, 68
 hyriid glochidia, 292, 293
 Limidae, 268
 Lymnaeidae as vectors, 1071
 Mathildidae on corals, 859
Pelseneeria, 623
 Pinnidae, 267
 of Polyplacophora, 175
 prosobranchs, 623
 Pteriidae, 262
 Pyramidellidae, 15, 867
 Pyramidelloidea, 865
Stilifer, 623
 parasitic mites, Hyriidae, 61
 paraspermatozoa, Fg 1.17, 20, 631,
 634, 708, 711, 713–716, 720,
 721, 724, 726, 727, 731, 735,
 737, 739
 Ampullarioidea, 634
 Caenogastropoda, 634
 Campaniloidea, 735
 Cerithioidea, Fg 15.82, 634, 707
 Conoidea, 634
 Cyclophoroidea, Fg 1.17, 634
 Cypraeoidea, 634
 functions, 20, 24, 634
 Janthinoidea, 634, 814
 Muricoidea, 634, 820
 Ptenoglossa, 808
 Scaliolidae, 733
 structure, 20
 taxonomic value, 20
 Tonnoidea, 634
 Triphoroidea, 634
Parastarte, 360
 brooding, 356
Parastrophia cygnicollis, 761
 external appearance, Fg 15.117
Parastrophia erseusi, 761
Parathyasira, 314
 endemism, 314
Parathyasira verconis, 314
Paratomoceras
 Devonian, 95
Paratomoceras lentiforme
 Devonian, Fg 1.98
 paratroch, trochophore, 591
Pardosinia, 360
 parental care, 25
Argonauta, 25
 Caenogastropoda, 637
 Calyptraeidae, 637
 Coralliophilinae, 637
 Cypraeidae, 637, 783
 Eulimidae, 637
 Gastropoda, 591
Hapalochlaena maculosa, 25
 Hipponicidae, 637
 Janthinidae, 637
 Littorinidae, 637
 Muricidae, 823
 Nacellina, 642
 Octopoda, 25, 469
 Opisthobranchia, 936
 Ostreidae, 270
 Ovulidae, 785
 Patellogastropoda, 637
Philippia, 591
 Philobryidae, 260
 prosobranchs, 637
 Siliquariidae, 637
 Trochidae, 637
 Vermetidae, 637
 Vetigastropoda, 637
 Pareorinae, 718
Parilimya, 399, 401, 405–407
 alimentary tract, 399
 siphons, 406
 statocysts, 406
 stomach, 406
 stomach type, 399
Parilimya fragilis, 399
 eggs, 407
 internal morphology, Fg 9.7
 prey capture, Fg 9.5
 statocysts, 406
Parilimya haddoni
 distribution, 404, 406, 407
 shell, Fg 9.7
Parilimya maoria, 399, 407
 statocyst, 406
Parilimya tasmanica, 406, 407
 distribution, 404, 406, 407
 habitat, 402
 shell, 406
 Parilimyidae, Fg 9.5, Fg 9.7, 226
 affinities, 407, 422
 characters, 406
 family treatment, 406
 genera, 405
 Parmacellidae, 1102
Parmacochlea fischeri, 1107
 parthenogenesis, 23, 634
 Caenogastropoda, 634
 Cerithioidea, 708
Deroceras laeve, 19
 Hydrobiidae, 634
Potamopyrgus antipodarum,
 19, 64, 588
 Stylommatophora, 589
Thiara, 588
 Thiaridae, 19, 65, 708, 727, 729
 Viviparidae, 634
Particondyla, 325
Particulazona, 182
Particulazona milnei, Fg 3.34, 182
Partula
 captive breeding, 112
 extinction on Moorea, 109
 Partulidae
 distribution, 1085
 gonoduct fusion, 1049
 Partuloidea, description, 1085
Parvamusium, feeding, 278
Parvaplustrum tenerum, 946
Parvilucina, haemoglobin, 313
Parvilucina tenuisculpta
 ctenidia, 311
 ctenidial microstructure, Fg 8.2
 feeding tube, 312
 habitat, 313
Parvilucina tenuisculpta
 ctenidial filament, Fg 8.3
Parvioris, diversity, 817
Parviterebra, shell, 827
Parviterebra brazieri, Fg 15.160
Parvithracia, 408
Paryphanta
 affinities, 1093
 Paryphantidae, 1091
Patella, 26, 581, 645, 646
 hermaphroditism, 633
 mantle cavity organs, Fg 14.16
 protandrous hermaphroditism, 23
 secondary gills, 579
 trochophore, Fg 1.1, Fg 14.34
Patella aspera, water loss, 625
Patella caerulea, pheromones, 635
Patella costulata
 Triassic, 645
 Siliquariidae, 637
 Triassic, 645
Patella fuenzalidai, 647
Patella peroni, breeding season, 24
Patella vulgata
 eye, Fg 15.19
 homing behaviour, 577
 pheromones, 635
 veliger, 26
 water loss, 625
Patellanax, 646
 Patellidae, Fg 1.1, Fg 1.14,
 Fg 14.16, Fg 14.34,
 Fg 15.19, Fg 15.34,
 Fg 15.35, Tb 15.1, 567, 639,
 641, 645
 family treatment, 645
 fossil record, 647
 lateral gills, 18
 on rocky shores, 29
 Patellina, Tb 15.1, 641
 description, 645
 Patellinae, characters, 645
 Patellogastropoda, Tb 14.1,
 Tb 15.1, 605, 606
 Aboriginal resources, 644
 apomorphies, 641
 Australian biogeography, 644
 circulation, 623, 624
 description, 639
 eyes, 629
 fertilisation, 631
 fossil record, 644
 habitat, 643
 intestinal length, 621
 kidney function, 625
 nervous system, 628
 nomenclature, 639
 oesophageal glands, 621
 osphradium, 630
 pedal glands, 612
 phylogeny, 640
 plants as substrata, 644
 podocytes, 627
 protandry, 633
 relationships, 609
 respiratory flow, 616
 sex reversal and territory, 633
 shell muscles, 613
 shell structure, 614, 640
 sperm morphology, 634
 statocysts, 630
 status, 567, 568
 stomach, 621
 subradular organ, 630
Patelloida, 639, 644, 652
 endemism, 652
 Miocene, 645
 radula, Fg 15.34
Patelloida alticostata, 652
 intraspecific competition, 31
Patelloida bellatula, 652
Patelloida calamus, 652
Patelloida cryptalirata, 652
Patelloida heteromorpha, 652
Patelloida insignis, 639, 652
Patelloida latistrigata, 31, 652
 interaction with barnacles, 31
Patelloida mimula, 652
 shell, Fg 15.40
Patelloida mufria, 32, 652
 commensalism, 32
Patelloida nigrosulcata, 652
 commensalism, 643
Patelloida saccharina, 652
 shell, Fg 15.40
Patelloida victoriana, 652
 Patelloidea, Tb 15.1, 639–641
 Aboriginal resources, 645
 biological monitoring, 645
 description, 645
 ecological research, 643
 phylogeny, 645
 as primitive group, 639
 taxonomic revision, 639
 Patelloididae, 652
 Patelloidinae, 641, 649
 in Australia, 652
 description, 651
 Tethyan origin, 652
Patina, 620
Patro, 281
 byssal notches, 280
 distribution, 281
Patro australis
 shell, Fg 6.20
Pattyclaya, 966, 967, 969
Pattyclaya arena, 968
Pattyclaya brycei, 968
 paua, 667
 paucispiral coiling
 operculum, Fg 15.6
Pauliella, 350
Pauropagma, Ordovician, 93
 pavilion
 Dentaliidae, Fg 10.3, Fg 10.10
 Scaphopoda, Fg 10.10, 433, 439,
 442, 444
Paziella, as fossils, 824
 pea shells, 59, 62, 352
 pearl formation and parasites, 262
 pearl mariculture, 73
 Pteriidae, 262
 pearl oysters, 13, 72, 225, 261

- pearl shell, 72
 fishery, 221
 pearlfish and *Pinctada*, 262
 pearls, 13, 72
 economic value, 73
 fishery, 221
 Hyriidae, 297
 Pteriidae, 262
 Unionoidea, 297
Peasiella, 738, 739
Peasistilifer, diversity, 817
Pecten, 198, 261, 277, 278, 418
 digestive rhythm, 209
 Jurassic, 97
 origin, 223
 pallial eyes, Fg 4.17, 213
 protandry, 215
 retina, 213
 statoliths, sensory cilia, Fg 4.18
Pecten alba, 275
Pecten fumatus, Fg 1.39, Pl 13, 275, 277
 catches, Fg 1.79
 fishery, Fg 1.81, 73, 220
 larval development, 28
 larval period, 277
 life span, 277
 nestling, 277
 shell, Fg 6.18
 State fisheries, Fg 1.80
Pecten maximus, 277
 larval cilia, 52
Pectenodoris, Fg 16.10
 radular teeth, Fg 16.10
Pectenodoris trilineata, 999
Pectinaria, 951
Pectindonta aupouria, 649
 Pectinidae, Fg 1.3, Fg 1.22, Fg 1.39, Fg 4.17, Fg 4.18, Fg 6.18, Fgs 1.79–1.81, Pl 5, Pl 12, Pl 13, 275
 catches, Fg 1.79
 in fisheries, 73
 as hosts to Capulidae, 774
 in seagrass, 39
 shell collecting, 76
 State fisheries, Fg 1.80
 Pectinina, description, 275
 Pectinodinae, 639
Pectinodonta, 648
 radula, Fg 15.34
 shell ultrastructure, 649
Pectinodonta aupouria, 649
Pectinodonta kapalae, 649
 shell, Fg 15.37
Pectinodonta morioria, 649
 Pectinodontinae, 641, 648
 deep-sea habitat, 648
 habitat, 648
 teeth, 648
 Tethyan distributions, 644
 Pectinoidea, 249, 275
 description, 275
 families, 275
Pectunculus aurifluus, 259
 mantle cavity, Fg 6.6
Peculator, 842
 endemism, 843
 rudimentary operculum, 842
Peculator hedleyi
 anatomy, Fg 15.170
 external appearance, Fg 15.170
 pedal disc, Gadilida, 433
 pedal elevator muscles, 347
 Crassatellidae, 326
 Donacidae, 346
 Trigoniidae, Fg 7.8
 pedal gape muscles
 Anomalodesmata, 399
 pedal gland
 and locomotion, 611, 612
 Vermetidae, 779
 pedal musculature
 Arcoidea, 205
 Bivalvia, 205
 Entalimorpha, 433
 Gadilimorpha, 433
 Phenacolepadidae, 700
 Protobranchia, 205
 Scaphopoda, 433
 Trigonoidea, 205
 Unionoidea, 205
 pedal nerve cords
 Gastropoda, 628
 pedal organ, Gastrochaenidae, 368
 pedal palp, Pholadidae, Fg 8.45
 pedal protractor muscles
 Cucullaeidae, Fg 6.3
 Donacidae, 347
 Galeommatidae, 316
 Limopsidae, Fg 6.5
 Philobryidae, Fg 6.7
 Trigoniidae, Fg 7.8
 pedal retractor muscle scars,
 Fg 8.40, 265, 410, 422
 Tridacnoidea, 332
 pedal retractor muscles, Fg 6.3,
 Fg 6.5, Fg 6.7, Fg 6.12,
 Fg 7.8, Fg 8.18, Fg 8.28,
 Fg 9.10, Fg 9.17, 251, 254,
 256–260, 265, 277, 295, 316,
 319, 323, 326, 333, 339, 345,
 349, 355, 362, 370, 406, 412,
 418–420, 422, 424,
 Anomalodesmata, 399
 Arcoidea, 253
 Arcticoidea, 348
 Bivalvia, Fg 4.5
 Heterodonta, 302
 Mactroidea, 336
 Scaphopoda, 433
 Solenioidea, 340
 pedal sinus
 Dentaliida, 433
 Gadilida, 433
 Scaphopoda, 433
 pedal-byssal retractor muscle
 Anomiidae, 280
 pedal-feeding, Fimbriidae, 313
Pedinogyra, 81, 1058, 1093
 external appearance, Fg 17.52
 habitat, 1052
 radula, Fg 17.52
Pedinogyra hayii
 reproductive tract, Fg 17.52
 Pedipedinae, 1078
 pediveligers, 28
 Bivalvia, 217
 Mimachlamys asperima, Fg 1.22
 morphology, Ostreidae, Fg 4.20
 Tellinoidea, 342
Pedum spondyloideum, Pl 12, 275, 277, 278
 peduncle lobes, Coleoidea, 466
Peelerophon, 93
Peelerophon oehlerti
 Ordovician, Fg 1.98
 pelagic mollusc shells
 as substratum, 49
 pelagic molluscs, 46
 Cephalopoda, 46, 49
 distribution, 80
 egg laying, 48
 Gymnosomata, 46
 holopelagic gastropods, 46
 larval development, 48
 meroplankton, 51
 pteropods, 46
 Thecosomata, 46
Pelagiella, Cambrian, 89
Pelagiella subangulata
 Cambrian, Fg 1.97
 Pelecypoda, 5
Pellicaria, 768
Pellicaria vermis, 768
 brooding, 769
 female genital ducts, Fg 15.122
Pellax, 677
 affinities, 677
 Pellibranchiata, 940
Pellibranchus cinnabareus, 996
 Pelsart, 6
 Pelseneer, 237
Pelseneeria
 diversity, 817
 parasitism, 623
Pelseneeria brunnea
 feeding, 817
 groups, 817
 shell, Fg 15.154
Peltarion
 as fossils, 695
 Peltospiridae
 fertilisation, 631
 nephridial gland, 626
 subradular organ, 630
 Peltospiroidea, affinities, 694
 Pelyciidae, affinities, 741
Pelycidion, 741
 pen, 453
 Coleoidea, 500
 pen shells, 265
Penaeus, 508
Pendaloma, 409
Pendaloma micans, 409
Pendroma, 692
 Pendromidae, Tb 15.1, 672
 family treatment, 692
Penepatella, 646
Penicillus, 413, 970
Penion, distribution, 827
Penion longirostris
 Tertiary, Fg 1.101
Penion mandarinus
 operculum, Fg 15.159
 radula, Fg 15.159
 shell, Fg 15.159
 penis
 Acteonidae, 934
 Anabathridae, 632
 Caenogastropoda, 632
 Coleoidea, 501
 Columbellidae, 632
 Emblandidae, 632
 Heteropoda, 632
 Hydrococcidae, Fg 15.118
 Lottiidae, 632
 Nautilidae, Fg 12.11
 Opisthobranchia, 934
 Pulmonata, 1050
 Rissooidea, Fg 15.118
 Pennatulacea, 38
 as nudibranch prey, 938
 as prey of *Armina* sp., 1008
 Pennsylvanian
 Pulmonata, 1057
Pepta, distribution, 846
 Peraclididae, Fg 16.63, 980
 family treatment, 983
Peraclis, 926, 982
 shell form, 923
Peraclis apicifulva, 984
Peraclis moluccensis, 984
Peraclis reticulata, Fg 16.63, 983, 984
 shell, Fg 16.63
Peraclis valdiviae, 984
Peratobelus
 Cretaceous, 99
 pericalymma larva, 52
 Aplacophora, 148
 lecithotropy, 53
 Nuculidae, 239
 Nuculoida, 235
 Protobranchia, 235
 Solemyidae, Fg 5.8, 243
 Solemyoidea, 235
 pericardial cavity
 Octopoda, 500
 Sepioidea, 500
 Teuthoidea, 500
 pericardial fluid, formation, 211
 pericardial glands
 Bivalvia, 211
 Cephalopoda, 463
 Coleoidea, 463
 Mollusca, 16
 Trigoniidae, 291
 Unionoidea, 291
Pericharax heteroraphis
 prey, *Notodoris gardineri*, 996
Periglypta, 358
 periostracum, 569
 Bivalvia, 201
 Crassatellidae, 301
 Cucullaeidae, 256
 Limopsidae, 258
 Lucinoidea, 301
 Noetiidae, 257
 terminology, 201
 Vesicomidae, 301
Periploma, 407–410
 burrowing, 403
 as fossils, 410
 mantle fusion, 398
Periploma fragile, 410
Periploma margaritaceum, 407
 burrowing, Fg 9.6, 403
 burrowing behaviour, 410
Periploma micans, 404, 409
 Periplomatidae, Fg 9.1, Fg 9.2, Fg 9.6, Fg 9.9
 burrowing, Fg 9.6
 characters, 408
 family treatment, 409
Periplomya, 412
Perisphinctes
 Jurassic, 97
 Peristerniinae, 833
 characters, 833
 peristome, Nautiloidea, Fg 12.3
 periwinkles, Pl 23, 683, 738
 perlemoen, 667
 Permian, 97
 Carditoidea, 322
 Crassatelloidea, 326
 fossil molluscs, Fg 1.99
 Hiatelloidea, 370
 marine transgressions, 91
 Orthocerida, 491
 Pholadomyoidea, 406
 Scaphopoda, 437
 permits for collection, 102
Permochiton
 as fossils, 176
 Permian, 178
Permochiton australianus, 97
 Permophoridae, 322
 distribution, 322
Perna, aerial respiration, 219
Perna viridis
 life span, 218
 reproduction, 218
Pernoceras, Devonian, 95
 Peronian Province, 78, 593

INDEX

- Peronian Region
 Cerithiopsidae, 811
 characteristic molluscs, 1057
 non-marine molluscs, 81
Perotrochus, 666
Perotrochus westralis
 euspermatozoa, Fg 1.17
Perrieria, 86, 1088
 distribution, 1088
Perrierina, 319, 320
 Perrierinidae, 318
Perrisodonta, 768
Persicula, 841
Persicula interruptolineata
 foregut, Fg 15.168
Persicula pulchella
 shell, Fg 15.167
 Personidae, Fg 15.140, Tb 15.1,
 792
 characters, 798
 family treatment, 798
 growth, 798
Personopsis, 799
Personopsis pusilla
 distribution, 799
 Perth Basin, Fg 1.95, 328
Pertusiconcha, 444
Peruvispira, Permian, 97
Peruvispira umariensis
 Permian, Fg 1.99
Pervicacia, alimentary tract, 850
 pest species, 1114
 Achatina fulica, Fg 17.21, 1055
 Achatinidae, 1089
 Arionidae in Europe, 1101
 Boonea impressa, 867
 Bradybaena similaris, 1055, 1115
 Candidula sp., 71
 Cernuella, 1114
 Cernuella virgata, 1055
 Cochlicella barbara, Fg 17.71,
 71
 Cochlicella spp., 1114
 Corbicula, 221
 Corbicula australis, 61
 Corbicula fluminea, 61
 Corbiculidae, 355
 Corbiculoidea, 353
 Cymatium martinianum, 802
 Cymatium muricinum, 802
 Cymatium nicobaricum, 802
 Cymatium parthenopeum, 802
 Helicidae, Fg 17.71, 1113, 1114
 Helicina orbiculata, 702
 Helicoidea, Fg 17.71
 Helix aspersa, Fg 17.71, 1114
 Limacidae, Fg 17.59, 1103
 Limacoidea, Fg 17.59
 Martesia striata, 374
 Milacidae, 1103
 Muricidae, 823
 Muricoidea, 820
 Notopala hanleyi, 63
 Octopus tetricus, 549, 550
 Pyramidellidae, 867
 Subulinidae, 1087
 Teredinidae, 374
 Theba pisana, Fg 17.71, 1114
 Vivipariidae, 107
 Zonitidae, Fg 17.22
 Zonitoides arboreus, Fg 17.22,
 1056
Petalifera, 935, 976
Petaloconchus, 779
 operculum, 779
 parental care, 637
Petaloconchus caperatus, 780
 as fossils, 780
Petaloconchus montereyensis
 spermatophore, Fg 15.129
 Petit, Nicolas-Martin, Fg 1.6, 7
Petrasma, 241
 petrels, lycoteuthid predators, 520
Petricola
 shell, 361
Petricola divergens
 distribution, 361
Petricola parvita, 361
Petricola pholadiformis
 hinge plate, Fg 8.39
 internal morphology, Fg 8.39
 shell, Fg 8.39
Petricola rubiginosa
 distribution, 361
 Petricolidae, Fg 8.39, 356
 family treatment, 361
Petroderma, 182
Pettancylus, 84
 Petterd, William, 8, 9, 1038, 1039
 Pfeiffer, H., 1038
Phacidoconcha
 Ordovician, Tb 1.6
Phacoceras, 491
Phacoides
 shell/body relationship, Fg 4.10
Phacoides pectinatus
 haemoglobin, 313
Phacosoma, 360
Phaenodesmia, Tb 1.6
 phagocytosis, 626
 Epimeniidae, 147, 156
 Scaphopoda, 434
 Phaliinae, 794
 characters, 795
Phalium, 795, 798
 distribution, 796
 habitat, 794
 varices, 794
Phalium pyrum
 on host shell, Fg 15.123
 Phanerobranchia, 990
 Nudibranchia, 990
Phanerophthalmus, Fg 16.16,
 954–956
 camouflage, 939
 organisation, Fg 16.1
Phanerophthalmus smaragdinus,
 Fg 16.35
 external appearance, Fg 16.35
Phanerotrema, Devonian, 95
Pharella, Aboriginal resources, 341
Pharidae, Fg 4.9, Fg 4.10, Fg 8.26,
 341
 family treatment, 341
Pharus, 341
Pharus legumen
 external appearance, Fg 8.26
Phasianella, 671, 678, 679
 distribution, 679
 endemic species, 679
 as fossils, 679
 operculum, 678
 shell, 678
Phasianella australis, 679
 headfoot, Fg 15.60
 radula, Fg 15.60
Phasianella dennanti
 as fossils, 679
Phasianella variegata, 679
 radula, Fg 15.60
Phasianella ventricosa, 679
 radula, Fg 15.60
 shell, Fg 15.60
 Phasianellidae, 673, 677
 Phasianellinae, 677
 in Australia, 673
 description, 678
 as octopod prey, 679
Phasianotrochus, distribution, 683
Phasianotrochus eximius
 shell, Fg 15.63
 use in jewellery, 683
Phasianotrochus irisodontes
 use in jewellery, 683
Phasmatopsis
 photophores, Fg 11.6
 Phasmidia, 68
Phaxas, 341
 pheasant shells, 673, 677, 678
 Phenacolepadidae, Fg 15.74,
 Tb 15.1, 610, 693, 700
 in Australia, 700
 family treatment, 700
Phenacolepas, 700
 habitat, 700
 prostate gland, 632
Phenacolepas calva
 distribution, 700
Phenacolepas crenulata
 distribution, 700
Phenacolepas immeritus
 distribution, 700
Phenacolepas mirabilis
 shell, Fg 15.74
Phenacolepas omanensis, 700
 anatomy, Fg 15.74
Phenacolepas tela, 700
Phenacovolva, 784
 distribution, 786
Phenacovolva carneopicta
 host, 786
Phenacovolva exigua
 as fossils, 786
Phenacovolva maccoyi, 784
Phenacovolva philippinarum
 distribution, 786
 host, 786
 pheromones
 Pulmonata, 1055
 spawning synchronisation, 635
Phestia darwini, Permian, Fg 1.99
Phestilla, 54, 939, 1015, 1016
Phestilla lugubris, Fg 16.11,
 Fg 16.20, 1016
 defensive glands, Fg 16.20
 jaw plate, Fg 16.11
Phestilla melanobranchia,
 Fg 16.107, Pl 36, 1016
 radula, Fg 16.102
Phestilla minor, 1016
Phestilla sibogae
 cue for settlement, 54
Phidiana, 1013, 1015
 organisation, Fg 16.1
Phidiana brocki, Pl 36
Phidiana newcombi, Fg 16.104,
 Fg 16.105
 external appearance, Fg 16.104
 organisation, Fg 16.1
 radula, Fg 16.105
Philine, Fg 16.3, 586, 926, 930,
 932, 935, 943, 951, 974
 diet, 937
 internal anatomy, Fg 16.3
 organisation, Fg 16.1
Philine angasi, Fg 16.4, Fg 16.10,
 Fg 16.14, Pl 33, 926, 950,
 951
 external appearance, Fg 16.4
 foregut morphology, Fg 16.14
 gizzard plates, Fg 16.14
 radular teeth, Fg 16.10
Philine aperta, 951
 nervous system, Fg 14.13
 predation, 583
Philine auriformis, Fg 16.10,
 Fg 16.14, Fg 16.16,
 Fg 16.18, 951
 gizzard plates, Fg 16.14
 nervous system, Fg 16.16
 radular teeth, Fg 16.10
 reproduction, Fg 16.18
Philine columnaria, Fg 16.29, 951
 external appearance, Fg 16.29
 shell, Fg 16.29
Philine denticulata, 950
Philine falklandica, Fg 16.14
 gizzard, Fg 16.14
 gizzard plates, Fg 16.14
Philine gibba, Fg 16.10, Fg 16.14,
 934, 936, 951
 gizzard plates, Fg 16.14
 radular teeth, Fg 16.10
Philine japonica, Fg 16.19, 951
 egg masses, Fg 16.19
Philine lima, shell, Fg 16.4
Philine marcusii, 951
Philine orca, 951
Philine orientalis, 951
Philine powelli
 nervous system, Fg 16.16
Philine umbilicata, shell, Fg 16.4
Philingwinea, 951
 Philinidae, Fg 14.13, Fg 16.4,
 Fg 16.10, Fg 16.14,
 Fg 16.16, Fg 16.18,
 Fg 16.19, Fg 16.29, Pl 33,
 926, 932
 egg mass, Fg 16.19
 evolution of body form, Fg 16.4
 evolution of shell, Fg 16.4
 family treatment, 950
 foregut morphology, Fg 16.14
 gizzard plates, Fg 16.14
Philinoglossa helgolandica, 951
Philinoglossa marcusii, Fg 16.30
 external appearance, Fg 16.30
 Philinoglossidae, Fg 16.30
 family treatment, 951
 Philinoidea, 940
 characters, 948
 evolution of shell form, Fg 16.4
 gizzard, Fg 16.14
 gizzard plates, Fg 16.14
 radular teeth, Fg 16.10
 reproduction, 934
Philinopsis, Fg 16.8, Fg 16.12,
 926, 937, 952
 alimentary tract, Fg 16.12
 haemocoel, Fg 16.8
 reproduction, Fg 16.18
Philinopsis giglioli, 952
Philinopsis taronga, Fg 16.4,
 Fg 16.31, 941, 952
 egg masses, Fg 16.31
 shell, Fg 16.4
Philinorbis, 951
Philippia, 862
 colour, 861
 as fossils, 862
 gonochorism, 862
 laboratory study, 862
 locomotion and shape, 575
 operculum, 861
 parental care, 591
Philippia krebsii
 development, 862
Philippia lutea
 egg laying, 862
 endemic, 861
Philippia oxytropis
 radula, Fg 15.183
 spermiogenesis, 862
Philippia radiata
 egg laying, 862
 egg mass, Fg 15.183
 operculum, Fg 15.183
 protoconch, Fg 1.58

- Phillip Island
extinction of molluscs, 114
- Philobrya*, 260
- Philobrya crenatulifera*, 260
distribution, 261
- Philobrya modiolus*, 260
distribution, 261
- Philobrya munita*, 260
- Philobryidae, Fg 4.16, Fg 6.7
family treatment, 260
- Philoxene*, Devonian, 95
- Phlyctaenachlamys*, 318
external appearance, Fg 8.8
- Phlyctaenachlamys lysiosquillina*
defensive tentacles, Fg 4.22
- Pholadidae, Fg 4.10, Fg 8.45,
Fgs 8.47–8.50, Pl 16, 371
as borers, 44
family treatment, 375
oviparity, 374
on reef slope, 35
subfamilies, 375
- Pholadinae, 375
- Pholadoidea, 226
description, 371
- Pholadomya*, 405, 406
circulatory system, 401
Cretaceous, Tb 1.6
fourth pallial aperture, 398
pedal gape muscles, 399
pedal retractor muscles, 406
siphons, 406
statocysts, 214, 406
stomach, 406
- Pholadomya candida*, 406, 413
feeding, 406
opisthopodium, 401
statocysts, 401
tentacle, 212
- Pholadomya maoria*, 406
- Pholadomya pacifica*, 406
- Pholadomya tasmanica*, 407
- Pholadomyidae, 226, 405
- Pholadomyoidea, 226, 405
- Pholadomyoidea
affinities, 422, 425
description, 405
families, 405
- Pholas*, 375
- Pholas obturamentum*, Pl 16
- Pholas orientalis*
external appearance, Fg 8.47
shell, Fg 8.47
- Pholidoteuthidae, Fg 11.25, 526
- Pholidoteuthis*, 526, 527
- Pholidoteuthis adami*
dermal cushions, 526
schooling, 527
- Pholidoteuthis boschmai*, 526
beak, Fg 11.25
- Phorinoplax*, Tb 1.6
- Phormium tenax*
Norfolk Island, 114
- Phos*
distribution, 827
- Phos senticosus*
operculum, Fg 15.159
radula, Fg 1.14, Fg 15.159
shell, Fg 15.159
- Phosphatoloricata, 176, 177
- Photinae, 827
- Photololigo*, 517, 520
shell, 517
- Photololigo chinensis*
age at maturity, 519
age determination, 519
captive breeding, 519
external appearance, Fg 13.9
hectocotylus, Fg 13.9
- photophores, Fg 11.6, Fg 11.20,
504, 520, 521, 523, 525, 529,
530, 531, 539
- Cephalopoda, 453, 454
courtship, Coleoidea, 501
- Octopoda, 545
- Oegopsida, 520
- Sepioidea, Fg 14.20
species recognition, 473
- Teuthoidea, Fg 11.6
- Vampyromorpha, 542
- photoreceptors, 401, 411, 412, 770
- Anomalodesmata, 401
- Bivalvia, 213
- Pandoroidea, 415
- Patellogastropoda, 640
- photoreceptors, siphonal, 404
- Thracioidea, 407
- photosensitive vesicles, Fg 11.20
- Coleoidea, 467
- photosynthesis
in Sacoglossa, 937
- phototaxis, 577
- Cleidotheriidae, 420
- Sepiadariidae, 510
- Stomatellinae, 685
- Phoxocephalidae
as molluscan predators, 39
- Phragmatopoma*
boring by *Hiattella*, 371
- phragmocone, 485
- Nautiloidea, Fg 12.3
- Phragmolites*, Silurian, 95
- Phragmorisma*, 408–409
ligament, 409
Oligocene, 409
- Phragmorisma watsoni*
distribution, 416
- Phrantela*, 63, 83
affinities, 755
distribution, Fg 1.91, 83
- phycobilin, 974
- Phyllaplysia*, 976
- Phyllaplysia taylori*, 976
reproductive system, Fg 14.30
- Phyllidia*, 1001
- Phyllidia ocellata*, Fg 16.85
external appearance, Fg 16.85
- Phyllidia varicosa*, 941
- Phyllidiella*, 1001
- Phyllidiella pustulosa*, Pl 35
- Phyllidiidae*, Fg 16.85, Pl 35, 990,
997
family treatment, 1000
prey, 926
- Phyllidioidea, 990
- Phylliroe*
external appearance, 926, 1006
as parasites of medusae, 1006
- Phylliroe bucephalum*, Fg 16.93
external appearance, Fg 16.93
- Phylliroidae, Fg 16.93
family treatment, 1006
light production, 48
in plankton, 47
- Phylloceras surya*
Cretaceous, Fg 1.100
- Phyllodesmium*, 940, 1013
- Phyllodesmium briareum*,
Fg 16.105
radula, Fg 16.195
- Phyllodesmium longicirrum*
zooxanthellae, 940
- Phyllodesmium serratum*,
Fg 16.105
radula, Fg 16.105
- Phyllodocidae, Fg 1.1
- Phyllomenia*
external features, Fg 2.10
reproduction, 154
- Phyllomeniidae, Fg 2.10
Bass Strait, 154
family treatment, 154
- Phyllonotus*
brooding, 823
- Phyllonotus regius*
parental care, 823
- Phyllopachyceras*
Cretaceous, 99
- phylogenetic schemes
Gastropoda, Fg 15.1
- phylogeny, 293, 336, 425, 940,
943,
Actinoceratoidea, Fg 12.2
Anomalodesmata, 404
Arcoida, 253
Bivalvia, 223
Cyliindrobulloidea, 947
dibranchiate cephalopods,
Fg 12.2
Discosoroidea, Fg 12.2
Endoceratoidea, Fg 12.2
Gastropoda, Fg 15.2, 606
Heterodonta, 305
Mactroidea, 337
Mollusca, Fg 1.4
Nautiloidea, Fg 12.2
Nautiloidea (subclass), Fg 12.2
Nautiloidea (superfamily),
Fg 12.10
Opisthobranchia, 940
Orthoceratoidea, Fg 12.2
Palaeoheterodonta, 293
Patellogastropoda, 640
Patelloidea, 645
Plectronoceratoidea, Fg 12.2
prosobranchs, 606
Scaphopoda, 437
subclass Nautiloidea, Fg 12.2
Thecosomata, 940
Tridacnidae, 336
Trochoidea, 672
Vampyroteuthis, 543
Verticordioidea, 420
- Physa*, 65, 70, 1074
mantle processes, Fg 17.35
- Physa acuta*, 64, 84, 1074
abundance in Murray River, 62
distribution and habitat, 64
filter blockage, 72
- Physa fontinalis*
reproduction, Fg 17.17
reproductive system, Fg 17.35
- Physalia*, 46, 51, 926, 938, 1015,
1017
and *Glaucus*, 925
as janthinid prey, 814
Tremoctopus defence, 51, 551
- Physastra*, 1074
as fossil, 1058
- Physastra rodingae*
as fossil, 1074
- Physella*, 1074
- Physella acuta*, 1074, 1075
distribution, 1075
shell, Fg 17.35
- Physeter catodon*, 538
- physical gill, pulmonates, 581
- Physicienne*, 162, 196, 568
- Physidae, Fg 17.17, Fg 17.35,
Tb 1.4, 84
family treatment, 1074
as fossils, 1057
in freshwater, 62
inland waters, 64
- Physoida*, 366
- Phytophthora*
transmission by molluscs, 72
- Pickfordiateuthis*, fin shape,
Fg 11.10
- Pickworthia*, 740
- Pickworthiidae, Fg 15.101,
Tb 15.1, 808
affinities, 703
family treatment, 739
- Pictodentalium*, 439
- Pictodentalium fomosum*, 439
shell, Fg 10.13
- Pictodentalium vernedei*
periostacum, 432
shell, 431
- piddocks, 371
- pigments
Bivalvia, 203
Corbiculidae, 203
Veneridae, 203
- Pila*, 637
- Pila ampullacea*
Angiostrongylus cantonensis, 69
- Pila polita*
Angiostrongylus cantonensis, 69
- pileworms, 371
- Pilidae, 706
- Piloceras*, 489
- Piloceratidae, 486
- Pilosabia*, 771
- Pilsbry, Henry August, 9, 162, 431,
639
- Pilsbrycharopa tumidus*, 1098,
1099
affinities, 85
- Pilsbryella*, 178
- Pilus*, 656
- Pinctada*, 262
host, *Sulcascaris sulcata*, 262
pearling, 13, 221
shell, 262
- Pinctada albina*, 262
fishery, 221
reproduction, 262
- Pinctada fucata*, 262
habitat, 262
reproduction, 262
shell, Fg 6.8
- Pinctada lata*, habitat, 262
- Pinctada margaritifera*, 262
conservation, 115
habitat, 262
heavy metals, 262
reproduction, 262
- Pinctada maxima*, Fg 1.78, 73, 262
conservation, 115
fishery, 221, 262
mariculture, 73
pearling, 72
and pinnotherid crabs, 262
- Pinna*, 265–267
as amathinid host, 869
as fossils, 267
and *Malleus meridianus*, 264
shell/body relationship, Fg 4.11
substratum for epibiota, 40, 44
Tertiary, 99
- Pinna bicolor*, Pl 11, 266, 267
age at sexual maturity, 267
in bioindicator system, 267
distribution, 267
external appearance, Fg 6.12
internal morphology, Fg 6.12
recruitment, 267
reproductive cycle, 266
shell, Fg 6.12, 265
shell regeneration, 266
- Pinna nobilis*, 266, 267
shell, 265
- Pinnidae, Fg 4.2, Fg 4.11, Fg 6.12,
Pl 11, 225
family treatment, 265

INDEX

- Pinnina, 261
Pinnocaris, Cambrian, 92
Pinnocaris robusta
 Ordovician, Fg 1.98, 93
Pinnoidea, 225
 description, 265
pinnotherid crabs and Pinnidae, 267
Pinufiidae, Fg 16.100, 1007
 family treatment, 1010
Pinufius, 1010, 1011
Pinufius rebus, Fg 16.100, 938,
 1010, 1011
 external appearance, Fg 16.100
Pipadentalium, 432
pipes, scaphopod shell, 433
pipis, Pl 15
 Donax deltooides, 347
 fishery, 76
 as *Paphies australis*, 340
Pirie-Torrens Basin, Fg 1.95
Pisania, 827
 distribution, 827
Pisanianura, 794, 798, 799
 affinities, 799
 characters, 799
 distribution, 799
 shell, 799
Pisanianura brevixaxis
 distribution, 799
 internal morphology, Fg 15.141
 shell, Fg 15.141
Pisanianura grimaldii,
 distribution, 799
 radula, Fg 15.141
 shell, Fg 15.141
Pisanianuridae, Fg 15.141,
 Tb 15.1, 792, 793
 family treatment, 799
Pisaniinae, 827
Pisidiidae, 352
Pisidium, 62, 82, 217, 355
 protandry, 215
 shell, 352
Pisidium aslini, distribution, 62
Pisidium casertanum, 62
 hinge, Fg 8.36
 reproductive rate, 218
 shell, Fg 8.36
 size, 217
Pisinna, 747, 749
Pisinna olivacea
 female genital system, Fg 15.106
 shell, Fg 15.106
Pisinna tropica, radula, Fg 15.106
Pisina zosterophila
 internal anatomy, Fg 15.106
Pitar, 355, 360
 distribution, 360
 diversity, 360
 habitat, 358, 360
Pitar citrinus
 shore zonation, Fg 1.45
Pitar subpellucidus
 siphonal coat, 357
Pitaridae, 356
Pitarinae, 356, 360
Pitta versicolor
 as pulmonate predator, 1054
Placamen, 358, 360
 as fossils, 339
 habitat, 358
 teeth, 356
 Tertiary, 101
Placamen berryi
 intertidal distribution, 43
 shore zonation, Fg 1.45
Placamen flindersi
 sculpture, 301
Placamen gravescens
 intertidal distribution, 43
 shore zonation, Fg 1.45
Placida, 973
Placida dentritica, 974
Placida fralila, 974
Placiphorella, 184
Placiphorella japonica, 184
Placiphorella velata, 165, 184
 behaviour, 165
Placiphorina, 184
Placopecten, swimming, 219
Placophora, 2
Placostylus, 1094, 1096
 affinities, 1057
 diversity, 86
Placostylus bivaricosus, 114
 external appearance, Fg 17.23
 probable extinction, 114
 shell, Fg 17.53
 threatened species, 114
Placostylus cuniculinsulae
 extinction, 114
Placuna, 281, 282
 distribution, 282
Placuna lobata
 internal morphology, Fg 6.21
 shell, Fg 6.21
Placuna placenta
 fishery, 282
 shell, Fg 6.21
Placunanomia, 280
Placunanomiinae, 281
Placunidae, Fg 6.21
Planorbis campanulatus
 distribution, 331
Plagiocardium frazeri
 distribution, 330
Plagioglypta, as fossils, 437
Plagioglypta iowaensis, 443
Plagiostoma
 Cretaceous, Tb 1.6
Plagiostromoceras, 491
Plagiostropha, 848
Plakobrachidae, Fg 16.47
 family treatment, 966
Plakobranthus, 966
 external appearance, 922
 relationships, 966
Plakobranthus ocellatus, Fg 16.47,
 941, 966, 967
 external appearance, Fg 16.47
Planaxidae, Fg 1.19, Fg 1.35,
 Fg 14.25, Fg 14.36,
 Fg 15.91, Tb 15.1, 729
 affinities, 709, 724, 730
 brood pouch, Fg 1.19
 cerithioid features, 722
 family treatment, 722
 reef intertidal shore, 36
 on rocky shores, 29
Planaxinae, 722
Planaxis, 722, 724
 distribution, 724
 metamorphosis, 591
Planaxis sulcatus, Fg 1.35, 23, 724
 brooding, 637
 distribution, 724
 external appearance, Fg 15.91
 host to trematodes, 724
 operculum, Fg 15.91
 possible cryptic species, 724
 protoconch, Fg 15.91
 radula, Fg 15.91
 shell, Fg 15.91
 stomach, Fg 14.25
Planktomya henseni, 219
 teleplanic larvae, 52
planktonic larvae
 development, 52
 predators, 53
planktonic molluscs
 as substratum, 49
planktotrophy, 22, 23
Bivalvia, 217
Caenogastropoda, 638
development phases, 54
Gastropoda, 592
Heterobranchia, 638
Neritopsina, 638
Opisthobranchia, 934, 936
Planorbarius, 65
 shell form, 64
Planorbarius corneus, 84
 distribution, 65
 embryogenesis, 1051
 reproduction, Fg 17.17
Planorbidae, Fg 1.71, Fg 17.17,
 Fg 17.33, Fg 17.34, Tb 1.1,
 Tb 1.4
 affinities, 1074
 Australian genera, 64
 economic importance, 66
 family treatment, 1072
 as fossils, 1057
 in freshwater, 62
 haemoglobin, 1047
 hosts for paramphistomes, 67
 inland waters, 64
 Miocene fossils, 84
 osmoregulation, 1045
 as potential vectors, 1056
 schistosome hosts, 68
 secondary gills, 18
 taxonomic status, 107
Planorbis campanulatus
 distribution, 65
plant pests, 71
plastids
 symbiosis in Sacoglossa, 937
platelets
 Aplacophora, 147
Platevindex, 1063
Platevindex chameleon
 external appearance, Fg 17.26
 penis, 1063
Platyceras
 Devonian, 95
 Silurian, 95
Platyceratidae
 and Patellogastropoda, 640
Platyclymenia, Devonian, 95
Platycolpus, 718
Platydemus manokwari
 impact on native fauna, 109
Platydidridae, 997
Platydidis sp., Fg 16.15
Platyhedyle, 961, 969
Platyhedyle denudata, Fg 16.51,
 969
 external appearance, Fg 16.51
Platyhedylidae, Fg 16.51
 family treatment, 969
Platynosomum fastosum, 70
Platyodon, 364
 adductor muscles, 364
 burrowing, 364
 shell, 364
Platyschides, 445
Platyteichum, Permian, 97
Platyteichum costatum
 Permian, Fg 1.99
Plaxiphora, 184
 Tertiary, 185
Plaxiphora albida, Fg 3.37, 172,
 175, 184–185
 habitat, 175
 homing, 175
 spawning, 173
Plaxiphora aurata, 184, 185
Plaxiphora australis, 184
Plaxiphora matthewsi, Pl 9, 185
Plaxiphora obscurella, 185
Plaxiphora paeteliana, 184
Plectotrema, 1078
Plectinoceras, 491
Plectodon, hinge teeth, 424
Plectoplites ambiguus
 as hyriid hosts, 293
Plectorhagada carcharias,
 epiphragm, Fg 1.62
Plectronoceratidae, 486
Plectronoceratoidea, 485
Plectronocera, 486
Pleioptygmatidae, 820
Pleistocene
 Australian pulmonates, 1058
 fossil record, 101
 Patellogastropoda, 644
 Scaphopoda, 437
 Tonnoidea, 794
Plesiocystiscus, radula, 840
Plesiotritoninae, 846
Plesiotrochidae, Fg 15.99, Tb 15.1,
 708, 718, 733
 family treatment, 735
 features, 736
 shell, Fg 15.99
Plesiotrochus, 733–735, 737
 affinities, 737
 habitat, 734
Plesiotrochus acutangulus, 735
Plesiotrochus cf. penitricinctus,
 737
Plesiotrochus crinitus, 735–737
 head-foot, Fg 15.99
 mantle cavity, Fg 15.99
 operculum, Fg 15.99
 radula, Fg 15.99
 spermatozoa, Fg 15.99
Plesiotrochus monachus, 736, 737
 Holocene, 737
 Pleistocene, 737
 shell, Fg 15.99
Plesiotrochus pagodiformis, 735,
 737
Plesiotrochus souverbianus, 735,
 737
Pleurehdera, 979
pleurembolic proboscis, Fg 15.12
 evolution, 619
 formation, 619
Pleurobranchaea, 938, 979, 980
Pleurobranchaea californica
 chemoreception, 577
 conditioning, 577
Pleurobranchaea maculata, 938,
 980
Pleurobranchaeinae, characters, 979
Pleurobranchella, 980
Pleurobranchidae, Fg 1.20,
 Fg 14.17, Fg 16.9, Fg 16.60,
 Pl 33, 940
 family treatment, 979
Pleurobranchinae
 characters, 979
Pleurobranchioidea, 979
 characters, 977
Pleurobranchomorpha, 940, 977
Pleurobranchus, 917, 925, 932,
 938, 980
 internal anatomy, Fg 16.3
Pleurobranchus grandis, 979
Pleurobranchus hilli, 941, 980
 egg mass, Fg 1.20

- Pleurobranchus membranaceus*,
Fg 16.9, 979
swimming, 925
- Pleurobranchus peronii*, Fg 16.60,
Pl 33, 941
external appearance, Fg 6.60
- Pleuroceridae, 729
affinities, 727
- Pleurodiscidae, Fg 17.43, Tb 1.5,
1082
family treatment, 1084
- Pleurodiscus balmei*
distribution, 1084
reproductive tract, Fg 17.43
shell, 1084
- Pleurodontinae, distribution, 1112
- Pleuroleuroidae, 1007
- Pleuromeris*, 324
- Pleuromerites*, as fossils, 275
- Pleuropegma*, Cambrian, 92
- Pleurophyllidia*, 1007
- Pleurophyllidiidae*, 1007
- Pleuroploca australasia*
shell, Fg 15.163
- Pleuroploca filamentosa*
as prey of *Conus omara*, Fg 1.30
- Pleuropoma*
in Australia, 702
distribution, 85
- Pleuropoma draytonensis*
distribution, 702
radula, Fg 15.77
shell, Fg 15.77
- Pleuropoma gladstonensis*
distribution, 702
- Pleuropoma gouldiana*
distribution, 702
- Pleuropoma jana*
distribution, 702
operculum, Fg 15.77
radula, Fg 15.77
- Pleuropoma macleayi*, habitat, 702
- Pleuropoma walkeri*
distribution, 702
- Pleuroprocta*, 1011
- Pleurotoichus*, Pl 35
- Pleurotomaria*, 631, 666
Cretaceous, 99
function of slit, 571
Jurassic, 97
- Pleurotomaria bassi*, 666
- Pleurotomaria midas*
radula, Fg 15.51
- Pleurotomaria quoyana*
radula, Fg 15.51
- Pleurotomaria tertiaria*, 666
- Pleurotomaria westralis*
shell, Fg 15.51
- Pleurotomariidae*, Fg 1.17,
Fg 15.51, Tb 15.1
in Australia, 664
family treatment, 665
pallial organs, 615
shell cleaning, 613
- Pleurotomarioidea, Tb 15.1, 664
description, 664
features, 610
mantle cavity, Fg 15.7
spiral caecum, 621
- Pleuroxia*, 56, 81
- plicate membranes
Mytilidae, 251
- plicatidium, 929
- Plicatula*, 273, 274
internal morphology, Fg 6.16
- Plicatula australis*, 274
- Plicatula chinensis*, 274
shell, Fg 6.16
- Plicatula muricata*, 274
- Plicatulidae, Fg 1.16, 273
family treatment, 273
- Plicatuloidea, 249
description, 273
- Pliocene, 712, 733
- Cephalaspidea, 956
fossil record, 101
- Patellogastropoda, 644, 645
- Rhytidoidea, 1091
- Sacoglossa, 961
- Scaphopoda, 437
- Tonnoidea, 794
- Plocamopherus*, 993, 994
bioluminescence, 994
- Plocamopherus ceylonicus*, 926
- Plocamopherus imperialis*, Pl 35,
926
- Plocamopherus naevatus*, 919
- Plotiopsis*, 65, 729
- plugs, scaphopod shell, 433
- Pneumoderma*, 987
- Pneumoderma atlanticum*, 986, 987
- Pneumoderma heronensis*, 987
- Pneumoderma macrochira*, 987
- Pneumoderma mediterraneum*, 987
- Pneumoderma spoeli*, 987
- Pneumodermatidae*, Fg 16.66,
Pl 34, 986
acetabuliferous arms, Fg 16.66
family treatment, 986
polytrochous larvae, Fg 16.66
- Pneumodermopsis*, 987
- Pneumodermopsis canephora*, 986,
987
- Pneumodermopsis heronensis*,
Pl 34
- Pneumodermopsis paucidens*,
Fg 16.66, 986, 987
distribution, 941
external appearance, Fg 16.66
- Pneumodermopsis spoeli*, Fg 16.66
external appearance, Fg 16.66
- pneumostome, 580
- Ampullariidae, 625
- Arionidae, 1100
- Cyclophoridae, 625
- Milacidae, 1103
- Pulmonata, 1037, 1039, 1046
role in water balance, 57
terrestrial taxa, 625
- podocyst, pulmonate embryo, 1051
- podocytes
Bivalvia, 211
Cephalopoda, 463
filtration, 627
Heterodonta, 303
Neomeniomorpha, 147
Polyplacophora, 169
- Pododesmus*, 280
ctenidia, 280
- Poirieria*, as fossils, 824
- poison gland, 585
Conoidea, 622, 819
derivation, 621
- Pojetaia*, 223, 306
as nuculoid, 223
prodissococonch, 223
shell features, 223
shell microstructure, 223
- Pojetaia runnegari*, 306
Cambrian, Fg 1.97, 89
- Polidevicia*, Tb 1.6
Carboniferous, 95
- Polinices*, 42, 612, 791
egg case, Fg 15.135
on sand plains, 38
Tertiary, 99
- Polinices conicus*
predator of *Paphies elongata*, 37
- Polinices duplicatus*
locomotion, 574
- Polinices incei*, egg mass, Fg 1.20
- Polinices mammilla*,
operculum, Fg 15.134
shell, Fg 15.134
- Polinices sordida*, locomotion, 574
- Polinicinae, 790
- pollution and bivalve fisheries
economic significance, 221
- Polyandrocarpa*
boring by *Hiatella*, 371
- Polybranchia*, 937, 969–971
- Polybranchia orientale*, 971
- Polybranchia pallens*, Fg 16.52,
941, 970, 971
egg masses, Fg 16.52
- Polybranchidae, 969
relationships, 940
- Polycera*, Fg 16.2, 993
external features, Fg 16.2
- Polycera capensis*, Fg 16.74, 941,
993
external appearance, Fg 16.74
introduced species, 940
- Polycera hedgpethi*, 941, 993
introduced species, 940
- Polyceratidae, 993
- Polyceridae, Fg 16.17, Fgs 16.74–
16.77, Pl 35, Pl 37, 990
external appearance,
Fgs 16.74–16.77
family treatment, 993
Kalininae, Fg 16.77
light organs, 994
Nembrothinae, Fg 16.76
radula, Fgs 16.74–16.77
rhizophore, Fg 16.17
status, 993
subfamilies, 993
Triophinae, Fg 16.75
- Polycerinae, 993
characters, 993
external appearance, Fg 16.74
- polychaetes
as larval predators, 53
as molluscan prey, 209, 797,
820, 823, 825, 829, 833, 850,
853, 867
- polychaete tubes, as food, 659
- Polychides gibbosus*, shell, 447
- Polydesma*
hinge, Fg 8.35
shell, Fg 8.35
- Polydesmia*, 488, 490
circulation, Fg 12.6, 488
- Polydora*, bio-erosion of molluscs,
44
- Polydora websteri*, 277
- Polyelasmocerae, Fg 12.4
- Polyelasmoceras*, 491
- Polygireulima*, brooding, 637
- polygoidal, 573
- Polygyridae
distribution, 1110
- Polygyris*, 1100
- Polygyroidea
description, 1110
families, 1110
- Polymesoda*, 354
habitat, 61
in middens, 355
pedal gape feeding, 354
shell, 352
size, 353
teeth, 354
- Polymesoda coxans*
distribution, 61
- Polymesoda erosa*, 354
- polymorphism
Batillaria australis, 722
- Polyodontes lupina*, 764
- Polyphysa*, 967
- Polyphysa peniculus*, 968
- Polyplacophora
aesthetes, 2
biogeography, 176
body cavities, 164
broadcast spawning, 25
brooding, 20
circulation, 167
classification, 177
definition and description, 161
direct development, 22
ecology and behaviour, 175
economic significance, 175
ect-aquasperm, 20
embryology, 173
excretion, 169
external features, Fg 3.2, 163
feeding and digestion, 2, 14, 165
fossil record, 88, 176
general features, 2, 12
history of discovery, 161
iteroparity, 29
larval development, 22
life history, 174
morphology and physiology, 163
muscular system and
locomotion, 164
natural history, 174
nervous system, 18, 170
Ordovician, 93
reef intertidal shore, 36
reproduction, 20, 172
respiration, 168
on rocky shores, 29
in seagrass, 38
sense organs, 18, 170
shell valves, 2
spawning, 20
Tertiary, 101
- polyploidy
Thiaridae, 729
- Polyschides*, 445
as fossils, 437
- Polysiphona*, 974
- polyspermy
Pulmonata, 1051
- polytrochous larva, Fg 16.66
- Pomacea*, effect on rice, 71
- Pomatias*, 611, 627
egg capsule, 636
kidney primordia, 627
- Pomatias elegans*
egg capsule, Fg 15.27, 637
locomotor wave patterns, Fg 14.9
reproduction, Fg 14.28
- Pomatiasidae*, Fg 14.9, Fg 14.28,
Fg 15.27, 606
locomotor wave form, 611
water balance, 56
- Pomatiopsidae*, Fg 15.112, Tb 1.4,
Tb 15.1
affinities, 746, 755
family treatment, 755
inland waters, 62, 65, 83
oviduct, 745
as *Schistosoma* host, 746, 756
taxonomic status, 107
- Pomatiopsinae*, 755
- Pomatiopsis*
affinities, 755
as fossils, 756
- Ponticeras*
Devonian, 95
- Popanoceras*, Permian, 97

INDEX

- population density
Batillariidae, 721
Bivalvia, 219
cyclones, 36
Galeommatidae, 219
Mactridae, 219
- Porites*, 54, 938, 939, 1011
as prey of *Phestilla* spp., 1016
as prey of *Pinufius rebus*, 1011
reef slope habitat, 35
- Porodorioidae, 990
- Poroleda*
diversity, 239
- Poromya*, 422-424
sensory papilla, Fg 4.18
siphonal tentacle, Fg 4.18
- Poromya* cf. *buttoni*
hinge, Fg 9.1
shell, Fg 9.17
- Poromya granifera*, 423
- Poromya granulata*, 422, 423
internal morphology, Fg 9.17
prey capture, Fg 9.5, 403
sensory structures, Fg 9.3
shell ultrastructure, 422
- Poromya illevis*, 423
distribution, 423
shell, Fg 9.17
- Poromya laevis*, 424
distribution, 423
- Poromyidae, Fg 4.18, Fg 9.1,
Fg 9.3, Fg 9.5, Fg 9.17
affinities, 422
family treatment, 422
sensory structures, Fg 9.3
septum, 209
- Poromyoidea, 226
affinities, 422
description, 422
- Porostomata, 990, 1001
- Porphyra*, 54
- porphyrins
Bivalvia, 203
Tricoliinae, 677
- Porpita*, Fg 1.49, 46, 926, 1015
as janthinid prey, 814
- Port du George, 196
- Port Phillip Basin, Fg 1.95
- Portlandia*, 240
- Posidonia*, 39, 737
habitat, 358
Jurassic, 97
- Posidonia australis*, Pl 7
- posterior adductor muscles
Bivalvia, Fg 4.1
Veneridae, Fg 4.1
- Posticobia*, 63, 83
distribution, 755
sculpture, 752
- Posticobia brazieri*
shell, Fg 15.111
- Posticobia norfolkensis*
extinct, 114
- Potamididae, Fg 1.47, Fg 14.3,
Fg 15.92, Fg 15.93, Pl 24,
Tb 15.1, 707
affinities, 718, 730, 732
characters, 724
family treatment, 724
physiological tolerance, 726
schistosome hosts, 68
- Potamidinae, 724
- Potamocorbula*, 366
- Potamopyrgus*, 63, 65, 634, 746
habitat, 755
ovoviviparity, 637
- Potamopyrgus acuta*
in filters, 72
- Potamopyrgus antipodarum*
abundance, 755
brooding, Fg 15.25, 637
distribution, 64, 83
in filters, 72
habitat, 64
impact on native fauna, 109
parthenogenesis, 19, 23, 634, 745
shell, 755
- Potamopyrgus niger*, 755
- Potamopyrgus nigra*, 755
- Poteriidae, Fg 14.22, 703
- Powelliphanta*, affinities, 1093
- Powellisetia*, distribution, 751
- Praecardium*, Devonian, 95
- Praecaryodes antiquata*, 1093
as fossil, Fg 17.24
- Praectenodonta raricostae*
as fossil, 241
- Praemeroceas*, Devonian, 95
- Praenuculidae, as fossils, 237
- Praeundulomya*, Permian, 97
- Pratulum*, 305, 331
distribution, 223
as fossil, 223
Tertiary, 101
- Pratulum probatum*
shell sculpture, Fg 4.3
- Praunus flexuosus*, 514
- Praunus inermis*, 514
- precision in sampling, 105
- predation, 533, 1106
adaptations, 583
Anomalodesmata, 209
Cephalopoda, 51, 471
in Gastropoda, 583
Heterodonta, 305
on Limacidae, 1102
in mangroves, 46
pallial lacunae,
Anomalodesmata, 401
pelagic molluscs, 48
Pulmonata, 1054
on rocky shores, 32
rodents, 58
Tellinoidea, 342
thrushes, 58
on tidal flats, 43
Tonnoidea, Fg 15.137, Fg 15.138
- Preiss, John, 8
- preservation
Aplacophora, 149
Carinarioidea, 804
Gymnosomata, 986
Opisthobranchia, 941
Pulmonata, 1060
techniques, 102
Thecosomata, 981
- prey
Carinarioidea, 622
Enoploteuthidae, 521
Idiosepiidae, 514
Loliginidae, 519
Muricidae, 823
- prey capture
Anomalodesmata, Fg 9.5, 403
Cephalopoda, 457
Coleoidea, 471, 474, 500
Conoidea, 622
Gastropoda, Fg 14.23
initiation, Coloeidea, 502
Octopoda, benthic, 458
Oegopsida, 458
Scaphopoda, 434
Sepioidea, 458
Septibranchia, 220
- prey detection
Pterotracheidae, 807
Septibranchia, 220
Vampyroteuthidae, 458
- prey groups, Caenogastropoda, 621
- prey immobilisation
Cephalopoda, 458
incirrute octopods, 458
Sepia, 458
- prey specificity
Neomeniomorpha, 151
- Primovula*, 784
- Primovula cruenta*
distribution, 786
host, 786
- Primovula helenae*
distribution, 786
egg mass, 785
host, 786
- Primovula pyriformis*
shell, Fg 15.131
- Primovula rhodia*, as fossils, 786
- Primovula verconis*
distribution, 786
- Prince Albert I de Monaco, 452
- Prionace glauca*
as argonautid predator, 554
- Prionodonta*, 249
- Prionovolvula*, Pl 6
- Prionovolvula brevis*, Pl 26
- Priscificus*
as fossils, 798
- Prisma*, 1064
generic status, 1064
- prismatic layer, Fg 4.7, 569
- Prisogasterinae, distribution, 673
- Pristiglomidae, characters, 237
- Pritchard, George B., 11, 101
- Privigna*, 358
- Proagorina*, 421
- Problacmaea*
parental care, 637
protandry, 633
- proboscis, 772, 807
- acrembolic, Fg 15.12
Architectonicoidea, 858
Caenogastropoda, Fg 15.12
and carnivory, 622
Conoidea, 846, 847
Eulimoidea, Fg 15.154
formation in prosobranchs, 619
Heterobranchia, Fg 15.186
Muricoidea, Fg 15.155, 819, 820
Naticoidea, 790
Neogastropoda, Fg 15.155,
Fg 15.160, Fg 15.162,
Fg 15.168, 610, 822
Ptenoglossa, 808
pleurembolic, Fg 15.12
Pyramidelloidea, Fg 15.186, 865
Scaphopoda, 434
Tonnoidea, Fg 15.138,
Fg 15.140, 792, 793
Triphoroidea, 808
- Procalpurnus*, 784
- Procentrium*, as veliger prey, 53
- procerebrum
Basommatophora, 1067
Eupulmonata, 1076
function, 1047
Pulmonata, 1047
Systellommatophora, 1060
- Procerovum batillans*, Tb 1.2
- Procerovum varium*, Tb 1.2
- Prochaetoderma*, 151
- Prochaetoderma yongei*
sexual maturity, 148
size, 148
- Prochaetodermatidae, Fg 2.6
family treatment, 151
- Proctonotidae, 1009
- Proctonotus*, 1009
- Prodenialium*, 439
as fossils, 437
- prodissoconch, 216
Bivalvia, 198
Condylocardiidae, 325
Galeommatidae, 316
Gryphaeidae, 269
Mytilidae, 251
Ostreidae, Fg 4.21, 270
Pandoridae, Fg 9.4
Philobryidae, 260
Pinnidae, Fg 1.59
Trigoniidae, 295
- prodissoconch I, 52
- prodissoconch II, 52
- Prohyria*, Triassic, 97
- Prohysteroceas*, Cretaceous, 99
- Prolixodens*, distribution, 811
- Prolixodens infracolor*
operculum, Fg 15.150
shell and protoconch, Fg 15.150
- Promantellum*, 268
- promyal chamber, Malleidae, 262
- promyal passages
Crassostreinae, 272
Gryphaeidae, 270
- Péron, François, Fg 1.5, 6, 161,
196, 236, 289, 549, 1038
- Proneomenia*, 155
- Proneomeniidae, Fg 2.12, 149
family treatment, 155
- Pronucula*, 237
- Pronucula vincentiana*, 237
- Propeamussiidae, 278
- Propeamussium*, 278
feeding, 278
- Propeamussium sensu stricto*, 278
- Propecuna subovata*, sculpture, 301
- Propeleda*, diversity, 239
- Prophysaon*
autotomy, 573
- Propilidiinae, 640, 641
in Australian waters, 649
characters, 649
subfamily treatment, 649
- Propilidium*
as fossils, 649
radula, Fg 15.34
- Propilidium ancyloides*, 649
- Propilidium pelseneeri*, 649
- Propilidium tasmanicum*, 643, 649
shell, Fg 15.38
- Propilidium teramachii*, 649
- Propopinoceras*
Permian, 97
- proprioceptors, Bivalvia, 213
- Proserpinellinae, 702
- Proserpinidae, 702
- Proserpininae, 702
- Prosinnia semperi*
distribution, 786
host, 786
- prosobranchs, Tb 15.1, 566, 605
alimentary tract, 616
circulation and respiration, 623
context of usage, 605
development and larvae, 637
excretion, 625
foot and locomotion, 611
generic diversity, 605
gonochorism, 631
gonoduct, 631
Heterobranchia, 854
iteroparity, 29
locomotion, 611
morphology and function, 611
Neogastropoda, 819
nervous system, 628
osmoregulation, 625
pallial organs, 615
phylogeny and classification, 606

- Ptenoglossa, 808
 regulatory detorsion, 614
 relationships, 605
 reproduction, 631
 shell and locomotion, 611
 torsion, 605
 traditional classification, 605
 Vetigastropoda, 664
 Prosopoecephalia, 432
 prostate gland, Fg 15.22, 632
 Caenogastropoda, 616
Protactinoceras, Fg 12.8, 489, 493
 connecting rings, 489
 phragmocone, Fg 12.8
 Protactinocerida, 489
Protactylocylmenia, Devonian, 95
Protaeolidiella atra, Fg 16.103
 radula, Fg 16.103
Protaeolidiella juliae, Fg 16.19
 egg masses, Fg 16.19
Protancylus
 affinities, 84
 protandry, 708, 1106
 Architectonicoidea, 859
 Bivalvia, 195
 Cerithioidea, 708
 Corbiculoidea, 215
 Galeommatoida, 215
 Gymnosomata, 588
 Opisthobranchia, 932
 Patellogastropoda, 642
 Pectinoidea, 215
 prosobranchs, 633
 Pulmonata, 1048
 Thecosomata, 588, 980
 Velutinoidea, 786
 Veneroidea, 356
 Xylophaga, 214
Protatlanta, shell, 804
 proteases, 209, 459, 1043
 protective behaviour
 Tridacnidae, 219
Proterato, 788
Proterato lachryma
 shell, Fg 15.132
Proterocamerocerina, 489
Prothalotia lehmanni, 672
Protobactrites, Silurian, 95
Protobarleeia, 746, 747
Protobarleeia myersi, 747
 radula, Fg 15.105
 protobranch gill
 Nuculoida, 235
 Solemyoida, 235
 Protobranchia, 224, 225
 characters, 225
 classification, Tb 5.1, 235, 237
 ctenidia, Fg 5.1
 description, 235
 digestion, 236
 elongation of gut, 235
 and lamellibranchs, 235
 Ordovician radiation, 223
 origins, 235
 shell features, internal, Fg 5.2
 statocyst, 214
 stomach, Fg 4.13
Protocanites, Carboniferous, 95, 97
 Protocardiinae, fossil record, 306
Protochiton, Tertiary, 177
Protochiton granulosus, Fg 3.28
 Protochitonidae, Fg 3.28, 176, 177
 protoconch, 13, 22, 739, 797, 808,
 816, 820
 Achatinoidea, Fg 17.48
 Architectonicoidea, 858
 Arionoidea, Fg 17.54
 Bactritoidea, 487
 Caenogastropoda, 638
 Cerithioidea, Fg 15.83, Fg 15.89,
 Fg 15.91, Fg 15.95, Fg 15.97,
 Fgs 18.85–15.87
 Cocculinoidea, Fg 15.44
 Gastropoda, Fg 14.36, 52, 591
 Lepetelloidea, Fg 15.47, 656
 Neritopsina, 638, 693
 Opisthobranchia, 915
 Orthoceratoidea, 487
 prosobranchs, 638
 Ptenoglossa, Fg 15.148
 pulmonate sculpture, 1039
 Pyramidelloidea, 865
 Rissoelloidea, 862
 Rissooidea, Fg 15.108, Fg 15.110
 Thecosomata, 981
 Tonnoidea, Fg 15.136,
 Fg 15.139, Fg 15.142, 792
 Triphoroidea, Fg 15.148
 Trochoidea, 672
 Valvatoidea, 855
 Velutinoidea, 787
 Vetigastropoda, 638
 Xenophoroidea, Fg 15.128
 protoconch I, 52
 protoconch II, 52
Protocrepidaria
 hinge teeth, 424
Protocypraea, as fossils, 784
 protogyny
 Bivalvia, 215
 Corbiculidae, 354
Protokionoceras, 491
 Protominae, 718
 protonephridia
 pulmonate embryo, 1051
Protonucula, 239
Protonucula verconis
 distribution, 239
 shell, Fg 5.5
Protopyrula capensis
 as fossils, 798
 protoplax
 Pholadidae, Fg 8.45, Fg 8.47
 protostyle, Fg 4.13
 Nuculidae, 237
 Scaphopoda, 434
Protothaca, 358
Prototomoceras
 Devonian, 95
 prototroch, 591
Protovirgus,
 Cretaceous, 99
 Triassic, 97
Protowenella, Cambrian, 92
Protowenella flemingi
 Cambrian, Fg 1.97
 prourine production
 Trigoniidae, 291
 Provalvatidae, ancestry, 856
Provanna, 621
 Provannidae, 708
Proxichione, 360
 as fossils, 360
Proximitra, as fossils, 843
Prunum aff. *aletes*
 foregut, Fg 15.168
Pruvotella, 988
 Pruvotinidae, Fg 2.1, Fg 2.11, 149
 family treatment, 154
 Psammobiidae, Fg 1.36, Fg 8.30,
 343
 family treatment, 345
Psephidia
 brooding, 356
 distribution, 360
 habitat, 360
Pseudamycla
 distribution, 829
 radula, 829
 shell, 827
Pseudamycla dermestoida
 shell, Fg 15.160
Pseudanachis
 radula, 829
 shell, 827
Pseudanachis duclosianus
 shell, Fg 15.160
Pseudarietites, Carboniferous, 97
Pseudavicula, Tb 1.6
 Cretaceous, Tb 1.6, 99
Pseudavicula anomala, Tb 1.6
Pseudavicula australis
 Cretaceous, Fg 1.100
Pseudavicula papyracea, Tb 1.6
Pseudaviculopectin, Tb 1.6
Pseudestea, 747
Pseudilbia, 959
Pseudiscus, 1100
Pseudobaylea, Permian, 97
Pseudobornella, 1002, 1003
 pseudobranchs
 Pulmonata, 1037
Pseudochama,
 distribution, 309
 shell, Fg 8.1
 shell cementation, 307
Pseudococculina, 662
 seminal groove, 663
Pseudococculina concentrica
 external appearance, Fg 15.46
Pseudococculina gregaria,
 Fg 15.50
 Pseudococculinidae, Fgs 15.45–
 15.50, Tb 15.1, 658
 family treatment, 661
 Pseudococculininae, 662
 pseudoconch
Corolla ovata, Fg 16.64
Cymbulia sibogae, Fg 16.64
 Cymbuliidae, Fg 16.64, 984, 985
 pseudocopulation, Epitoniidae, 816
 pseudo-ctenolial tooth
 Propeamussiidae, 278
 pseudo-ctenolium
 Entoliidae, 279
 Pectinidae, 275
Pseudocypraea adamsonii
 radula, Fg 15.131
 Pseudodorididae, 992
 pseudofaeces
 Anomioidea, 280
 Chamidae, 308
 Corbulidae, Fg 8.42, 366
 Crassostreinae, 272
 Cyamiidae, 320
 Fimbriidae, Fg 8.4, 314
 Lophinae, 272
 Mactroidea, 337
 Martesiinae, 375
 Myidae, Fg 8.41
 Ostreinae, 270
 Pholadoidea, 372
 Tridacnidae, 333
Pseudoglossus
 distribution, 239
Pseudohedenstroemia, Triassic, 97
 pseudohermaphroditism
 Buccinidae, 827
 Nassariidae, 831
Pseudoilbia lineata, 959
Pseudoilbia mariana, 959
Pseudoischnochiton, 176
Pseudolimea, Tb 1.6
Pseudoliotia, 764
Pseudoliotia micans, 764
 radula, Fg 15.119
 shell, Fg 15.119
Pseudoliotia speciosa
 external appearance, Fg 15.119
Pseudoliotina, 673
 Pseudolividae, 835
 Pseudolivinae, 835
Pseudomalaxis
 distribution, 862
 as fossils, 862
Pseudomalaxis thetidis
 shell, Fg 15.183
 Pseudomelatominae, 850
Pseudomyalina, Permian, 97
Pseudomyona, Cambrian, 89
Pseudomyona queenslandica
 Cambrian, Fg 1.97
 pseudo-operculum
 in land snails, 571
 Stylommatophora, 1079
 pseudopallium, Eulimidae, 817
Pseudophilina, 951, 952
Pseudophyllites, Cretaceous, 99
Pseudopisina, 743
Pseudopisina costata
 radula, Fg 15.102
Pseudopisina gregaria, 743
 operculum, Fg 15.102
 shell, Fg 15.102
Pseudopotamis, 729
 pseudoproboscis
Calliostoma, 617
 Capulidae, 774
 Turbinidae, 673
 Turbininae, 675
Pseudoringicula, 946
Pseudorthoceras, 491
Pseudoschistoceras, Permian, 97
 pseudo-shell
 Asperspinidae, 960
Pseudoskenella
 distribution, 867
 shell, 867
Pseudoskenella depressa
 shell, Fg 15.186
Pseudostomatella, 684
Pseudosuccinea, 65
Pseudosuccinea columella, 64, 70,
 83, 1070
 distribution, 1071
 fasciolosis, 67
 shell, Fg 17.31
 as vector of *Fasciola hepatica*,
 64, 1071
 as vector of liver fluke, 64, 1071
 in Western Australia, 67
 Pseudothecosomata
 characters, 47, 980
 external appearance, 923
Pseudotindaria, 239
Pseudotoites, Jurassic, 97
Pseudotonicia cuneata, 165
 habitat, 175
Pseudotorinia, as fossils, 862
Pseudotorinia colmani
 endemic, 861
Pseudotricula eberhardi, 112
 in caves, 755
Pseudotritonia, 1008
Pseudotritonia gracilidens,
 Fg 16.97, 1009
 external appearance, Fg 16.97
Pseudovertagus, 712
Pseudovertagus aluco
 shell, Fg 15.83
 Pseudowutinoceratidae, 490
Psilaxis, 862
 Psilostomatidae, 67
Pseudoschnochiton, Tertiary, 179

INDEX

- Ptenoglossa*, Tb 15.1, 610, 620, 632, 703
description, 808
hermaphroditism, 633
superfamilies, 808
synapomorphies, 808
taxa, 703
- ptenoglossate radula*, 582, 811
Eulimoidea, 813
- Pteraeolidia*, 1015
- Pteraeolidia ianthina*, Fg 16.104, Fg 16.105, Pl 4
external appearance, Fg 16.104
radula, Fg 16.105
- Pteraeolidiinae*, Fg 16.104, Fg 16.105, 1015
- Pteria*, 262
as amathinid host, 869
form, 261
habitat, 262
pearling, 221
- Pteria heteroptera*, shell, Fg 4.2
- Pteria penguin*
habitat, 262
internal morphology, Fg 6.8
shell, Fg 6.8
- Pteria saltata*, Pl 11
- Pteriidae*, Fg 1.78, Fg 4.2, Fg 6.8, Pl 10, Pl 11, 13, 225
family treatment, 261
genera, 262
on reef conglomerate, 36
- Pteriina*, 261
- Pterinea*, Tb 1.6
Ordovician, 92
- Pterinopecten*
Devonian, 95
- Pterioidea*, 249
characters, 225
description, 261
mantle folds, 250
- Pterioidea*, 225, 249
description, 261
families, 225, 261
- Pteriomorphia*, 225
description, 249
nacre, 202
orders, 249
possible stem, 95
statocyst, 214
- Pterochelus*, 823
- pteroenone*, 48
- Pteronitella*, Silurian, Tb 1.6
- Pteronychida*, Tb 1.6
- pteropod ooze*, 49, 980
- pteropods*, 922
as pterotracheid prey, 807
- Pteropsellinae*, 337
- Pteropurpura*, Tertiary, 99
- Pterosoma*, characters, 807
- Pterosoma planum*
external appearance, Fg 15.146
shell, Fg 15.146
- Pterotrachea*, 807
- Pterotrachea coronata*
distribution, 808
feeding, 807
gills, 808
radula, Fg 15.147
- Pterotrachea hippocampus*
distribution, 808
external appearance, Fg 15.147
gills, 808
- Pterotrachea scutata*
distribution, 808
external appearance, Fg 15.147
gills, 808
- Pterotracheidae*, Fg 15.147, Tb 15.1, 613
abundance, 808
as carinariid prey, 806
family treatment, 807
in plankton, 47
- Pterotrigonia*, Cretaceous, Tb 1.6
- Pterygia*, distribution, 842
- Pterygia crenulata*, shell, Fg 15.169
- Pterygioteuthis*,
photophores, Fg 11.6
suckers, 521
- Pterygioteuthis gemmata*, 521
breeding season, 521
external appearance, Fg 13.11
- Pterygioteuthis giardi*, 521
- Pterynotus*
as fossils, 824
shell, 823
Tertiary, 99
- Pterynotus triformis*, 570
function of apertural lip, 571
- ptyaline gland*
Dendrodorididae, 1000
Phyllidiidae, 1001
- Ptychactractinae*, 825
- Ptychobela*, 848
- Ptychoceras*, Cretaceous, 99
- Ptychodera flava*
as terebrid prey, 850
- Ptychomphalina*, Permian, 97
- Ptychopegma*, Ordovician, 93
- Ptychopteria*, Devonian, Tb 1.6
- Ptychorhytida*
radular function, 583
- Ptychosphaera*, Devonian, 95
- Pseudotorinia*, diversity, 861
- Pugilina*, distribution, 832
- Pugilina cochlidium*
distribution, 832
head, Fg 15.162
operculum, Fg 15.162
radula, Fg 15.162
shell, Fg 15.162
- Pugnus*, 841, 946
- Pugnus parvus*, radula, Fg 15.167
- Pulicicochlea calamaris*
feeding, 584
- pulmonary cavity*
Amphibolidae, 1067
Cionellidae, 1081
Lymnaeidae, Fg 17.33
Planorbidae, Fg 17.33, 1072
Pulmonata, Fg 17.39, 1037, 1044, 1046
- Pulmonata*, Fg 17.20, 566, 607, 854,
age at maturity, 29
aquatic groups, 580
Basommatophora, 1067
behaviour, 1055
biogeography, 1056
body shape, 1039
characters, 1037
circulation, 1044
classification, 1060
collection of specimens, 1058
definition and description, 1037
ecology, 1052
economic significance, 1055
egg masses, 25
embryology, 1051
excretion, 1045
feeding and digestion, 1042
fossil record, 1057
hermaphroditism, 20
history of discovery, 1038
iteroparity, 29
laboratory culture, 1060
life history, 1051
locomotion, 1042
- Pulmonata*, 1039
methods of study, 1058
musculature, 1041
natural history, 1051
nervous system, 1047
orders, 1037
paraphyly, 854
polyphyly, 1037
preservation and storage, 1060
radular preparation, 1060
relaxation of specimens, 1059
reproduction, 1048
respiration, 1046
semelparity, 29
sense organs, 1047
shell, 1039
Sigmurethra, 1086
slug body forms, Fg 17.58
status, 568
Systellommatophora, 1060
transport of live animals, 1059
type localities, 1038
water conservation, 1055
- pulmonate predators*
Testacella haliotidea, 1056
- Pulsellidae*, 444
- Pulsellum*, 444
- Pulsellum adelaidense*, 445
- Pulsellum eboracense*, 444
shell, 446
- Pulsellum lofotensis*
egg detachment, 436
spawning, 436
yolk granules, 436
- Pulvinitidae*, Fg 6.11, 225
family treatment, 265
- Pumilicopta*, 1084
shell, 1082
- Pumilicopta bifurcata*, Fg 17.42
apertural dentition, Fg 17.42
- Punctabyssia*, 662
- Punctacteon*, 943, 944
- Punctacteon flammea*, 944
- Punctidae*, Fg 17.3, Fg 17.54, Tb 1.5, 86
family treatment, 1096
on Lord Howe Island, 114
- Punctum*, 1097
- Puncturella*, 669
- Puncturella noachina*
hermaphroditism, 633
- Pupa*, Fg 16.16, 924, 927, 932, 934, 943, 944
nervous system, Fg 16.16
- Pupa kirki*, Fg 16.7, Fg 16.11, Fg 16.12, 935–937
alimentary tract, Fg 16.12
epidermal glands, Fg 16.7
jaw plate, Fg 16.11
- Pupa nitidula*, Fg 16.21, 944
external appearance, Fg 16.21
shell, Fg 16.21
- Pupa solidula*, 944
- Pupa sulcata*, Fg 16.21
evolution of body form, Fg 16.4
external appearance, Fg 16.4, Fg 16.21
shell, Fg 16.21
- Pupilla*, 86, 1084
- Pupillidae*, Fg 1.92, Fg 14.4, Fg 17.3, Fg 17.42, Tb 1.5, 85, 86, 1082
apertural dentition, Fg 17.42
family treatment, 1082
- Pupillinae*, genera, 1084
- Pupilloidea*
description, 1082
families, 1082
- Pupina*, 705
- Pupina bidentata*, 705
- Pupina coxeni*, Fg 1.61
external appearance, Fg 15.79
- Pupina meridionalis*
shell, Fg 15.79
- Pupina (Signepupina)*, shell, 705
- Pupina thomsoni*, 705
radula, Fg 15.79
shell, Fg 15.79
- Pupinella*, 705
- Pupinella (Necopupina)*, shell, 705
- Pupinella planilabris*
shell, Fg 15.79
- Pupinella simplex*
breathing pore, 580
breathing tube, Fg 14.18
- Pupinellinae*, 705
- Pupinidae*, Fg 1.61, Fg 14.18, Fg 15.79, Tb 1.5, Tb 15.1, 703
affinities, 86
family treatment, 704
- Pupininae*, 704, 705
- Pupisoma*, 1084
habitat, 1052, 1082
shell, 1082
- Pupisoma circumlitum*, Fg 17.42
sculpture, Fg 17.42
shell sculpture, Fg 17.3
- Pupisoma orcula*, radula, Fg 17.42
- Pupoides*, 86, 1084
distribution, Fg 1.92
shell, 1082
- Pupoides adelaidae*
distribution, Fg 1.92
water balance, 1082
water retention, 1084
- Pupoides beltjanus*
distribution, Fg 1.92
- Pupoides pacificus*
distribution, Fg 1.92
shell, Fg 17.42
- 'purple' gland*, Anaspidea, 974
- Purpurocardia purpurata*, 324
- Pusia*, 844
- Pusillina*
distribution, 751
- Pusillina marmorata*
radula, Fg 15.108
- Pustularia*, 780
- Putilla*
radula, Fg 15.69, 691
shell, 691
- Putilla translucida*, shell, Fg 5.69
- Pycnoceras*, 491
- Pycnodonte*
Cretaceous, Tb 1.6
as fossils, 270
- Pycnodonteinae*, description, 269
- Pygmanisus*, 1074
distribution, 84
shell form, 65
- Pygmipanda*, 1093
- Pyramidella*, 867
habitat, 867
locomotion and shape, 576
- Pyramidella acus*, head-foot, 866
- Pyramidella dolabrata*
columellar folds, Fg 14.12
external appearance, Fg 14.12
- Pyramidellidae*, Fg 14.12, Fg 15.186, Tb 15.1, 854
affinities, 865
as calyptraeid predators, 774
characters, 606
diet, 42
epibiotia, 44
family treatment, 865
hermaphroditism, 633
as parasites, 38, 42

- relationships, 566, 606
on sand plains, 38
- Pyramidelloidea, 946
- Pyramidelloidea, Tb 15.1
description, 865
as parasites, 865
- Pyramus, Permian, 97
- Pyramus barringtonensis
as fossils, 405
- Pyramus laevis, as fossils, 405
- Pyrazus, 720, 721
- Pyrazus ebeninus, Fg 1.48,
720–722
Aboriginal resources, 722
desiccation, 722
distribution, 79, 593, 721
external appearance, Fg 14.3
operculum, Fg 15.90
radula, Fg 15.90
shell, Fg 15.90
- Pyrene, shell, 827
- Pyrene bidentata
habitat, 829
omnivory, 829
- Pyrene turturina, shell, Fg 15.160
- Pyrgopsis pacificus, 540
- Pyropelta, feeding, 658
- Pyropelta musaica, Fg 15.50
- Pyropeltidae, Fg 15.48, Fg 15.50,
653, 658
- Pyroteuthinae, characters, 521
- Pyroteuthis
hectocotylus, 521
hooks, 521
- Pyroteuthis margaritifera, 521
external appearance, Fg 13.11
radula, Fg 13.12
- Pyrunculus, 949, 950
- Pyrura stolonifera, Fg 1.23
- Pythia, 1078
genital ducts, 1078
habitat, 1078
reproductive morphology, 20
shell, 1078
shell modification, Fg 14.6
- Pythia scarabaeus
genital duct, 1048
shell, Fg 17.37
- Pyura, 175
- Pyura stolonifera
as ranellid prey, 800
- Pyxipoma, 720
brooding, 637
mantle cavity, Fg 15.89
- Pyxipoma weldii
head-foot, Fg 15.89
morphology, Fg 15.89
protoconch, Fg 15.89
radula, Fg 15.89
- 
- Quadrilatera, 257
- quantitative ecological sampling,
104
- Quaternary
Acrosterigma reeveanum, 331
Australian pulmonates, 1058
fossil record, 101
Heterodonta, 306
Lord Howe Island, 1058
queen conch, 768
queen scallop, Pl 13, 73, 277
- Quenstedtia, Jurassic, 97
- Questimya, 423
- quick muscle, Bivalvia, 204
- Quiros, 1096
- Quishugoceras, 493
- Quoy, Jean R.C., 7, 162, 196, 289,
499, 919, 1038
- 
- rachidian tooth, 14
- Rachiglossa, 620
- rachiglossate radula, Fg 1.14, 582,
819
- Rachispeculum, 1085
- radial mantle glands
see mantle glands
- Radianthidae
as molluscan predators, 42
- radiation
Arcoida, 253
Camaenidae, 1112
Gastropoda, 605
Heterodonta, 306
Hydrobiidae, 754
Lucinoidea, 310
Muricoidea, 820
Myoidea, 306
Neogastropoda, 819
Opisthobranchia, 940
Protobranchia, 235
Pteriomorpha, 250
Tellinoidea, 306
Veneroidea, 306, 307
- Radiocondyla, 325
- Radix, affinities, 1071
- Radsia nigrovirens, 185
- radula, 707, 711, 782, 794, 798,
799, 817, 983, 985, 988, 997,
1002, 1106
Achatinelloidea, Fg 17.40, 1080
Achatinoidea, Fgs 17.47–17.49,
1087
Acochlidia, 959
Amphiboloidea, Fg 17.30, 1067
Ampullarioidea, Fg 15.81, 706
Aplacophora, 147
Architectonicoidea, Fg 15.182,
Fg 15.183, 858
Arionoidea, Fg 17.54, Fg 17.56,
Fg 17.58
Avacoidea, Fg 17.52
Bulimuloidea, Fg 17.53
Bulloidea, 957
Calyptraeidea, Fg 15.126
Camaenoidea, 1112
Camenoidea, Fg 17.69
Campaniloidea, Fg 15.98,
Fg 15.99, 734
Capuloidea, Fg 15.127
Carinariidea, Fgs 15.145–
15.147, 804
Cephalopoda, 453, 459
Cerithioidea, Fg 15.83,
Fgs 15.85–15.87, Fg 15.89,
Fg 15.90, Fgs 15.93–15.97
Chaetodermomorpha, 150
Cingulopsoidea,
Fgs 15.102–15.104
Cionelloidea, Fg 17.41, 1081
and classification, 620
Cocculiniformia, 654
Cocculinoidea, 656
Coleoidea, 500
Conoidea, 846, 847
Cypraeoidea, Fg 15.130,
Fg 15.131, 780
Ellobioidea, Fg 17.37
feeding mode, 15
Fissurelloidea, 669
flexoglossate, 619
formation in prosobranchs, 617
function in prosobranchs, 617
- Gastropoda, 582
Glacidorboidea, Fg 17.36, 1075
Gymnosomata, 986
hardening, 620
Helicoidea, Fg 17.71, Fg 17.72,
1113
Janthinoidea, Fg 15.151
Lepetelloidea, Fg 15.48, 658
Lepetopsina, 648
Limacoidea, Fgs 17.60–17.65,
1102
Littorinoidea, Fg 15.100
Lymnaeoidea, Fgs 17.31–17.33,
1069
morphology, 14
Muricoidea, 819, 820
Naticoida, Fg 15.134, Fg 15.135
Neogastropoda, Fg 15.158,
Fg 15.159,
Fgs 15.162–15.167,
Fgs 15.169–15.171, 822
Neritoidea, 694
Neritopsina, Fg 15.73, Fg 15.77
Octopoda, Fg 11.13,
Fgs 13.35–13.38
Omaliogyroidea, Fg 15.185, 864
Onchidioidea, Fg 17.26, 1063
Opisthobranchia, Fg 16.74, 582,
926
Otinoidea, Fg 17.25, 1062
Partuloidea, Fg 17.45, 1085
Patellogastropoda, Fg 15.34,
639, 641
Pleurotomarioidea, 665
Polygyroidea, Fg 17.68, 1110
Polyplacophora, 166
preparation, 103
preservation, 942
Ptenoglossa, Fg 15.149,
Fg 15.150, 808
ptenoglossate, 811
Pulmonata, Fg 17.10, 582, 1037,
1043
Pupilloidea, Fg 17.42, Fg 17.44,
1082
rachiglossate, 819
Rathouisioida, Fg 17.27,
Fg 17.28, 1064
rhinoglossate, 810
Rhytidoidea, Fg 17.51, 1091
Rissoelloidea, Fg 15.184
Rissooidea, Fg 15.116,
Fgs 15.105–15.114,
Fgs 15.118–15.120, 745
Sacoglossa, 961
Scaphopoda, Fg 10.8, 431, 434
Seguenzioidea, 692
Sepioidea, Fg 13.3, Fg 13.4,
Fg 13.7, Fg 13.8, 504
Siphonarioidea, 1067
Streptaxoidea, Fg 17.50, 1090
Stromboidea, Fg 15.121,
Fg 15.122, 766
structure and function, 582
structure in Coleoidea, 500
Succinoidea, Fg 17.67
Systellommatophora, 1060
taenioglossate, 610
teeth, 14
Teuthoidea, Fg 13.9, Fg 13.10,
Fgs 13.12–13.27, 515
Thecosomata, 980
Tonnoidea, Fgs 15.136–15.138,
Fgs 15.140–15.144, 792, 793
toxoglossate, 819, 846
Trimusculoida, Fg 17.38
Triphoroidea, Fg 15.149,
Fg 15.150
Trochoidea, 671, 672
Valvatoidea, Fgs 15.179–15.181,
854, 856
Vanikoroidea, Fg 15.123,
Fg 15.124
Velutinoidea, Fg 15.132,
Fg 15.133, 786
Vermetoidea, 778
- Vetigastropoda, Fgs 15.51–
15.70, 605, 675
- Xenophoroidea, Fg 15.128
- radula preparation
Pulmonata, 1060
- radular bolsters
Dentaliidae, Fg 10.7
Scaphopoda, Fg 10.7
- radular caecum, 620
- radular evolution
Conidae, 622
Turridae, 622
- radular function
Chaetodermatidae, 150
Gastropoda, Fg 14.22, 582
Janthinidae, 811
Lymnaeidae, Fg 17.9
Prochaetodermatidae, 150
Pulmonata, Fg 17.9, 1043
- radular oligomerisation, 620
- radular sac
coiling, 620
pulmonate embryo, 1051
- radular structure, 14
Acmaeoidea, 641
Gastropoda, Fg 1.14
Nacelloidea, 641
Opisthobranchia, Fg 16.10
Patellogastropoda, 641
Patelloidea, 641
- radular teeth
Aglajidae, Fg 16.10
Cylichnidae, Fg 16.10
Gastropteridae, Fg 16.10
Lepetidae, 649
Philinidae, Fg 16.10
Philinoidea, Fg 16.10
strength and diet, 620
structure, 582, 620
- radular types, 582
docoglossate, 619
rhipidoglossate, 620
stereoglossate, 619
taenioglossate, 620
- Raeta, 337
- rainforest
effects of clearing, 107
habitats, Fg 1.102
molluscan diversity, 107
- Ranella
Tertiary, 101
- Ranella australasia, 800, 801
egg mass, 793
reproduction, Fg 15.143
shell, Fg 15.142
- Ranella intercostalis
as fossils, 801
- Ranella olearia
distribution, 801
- Ranella olearium
alimentary tract, Fg 15.143
- Ranellidae, Fg 1.31, Fg 14.1,
Fg 15.142, Fg 15.143,
Tb 15.1, 26, 35, 792, 798
family treatment, 799
shell features, 800
- Ranellinae, 799
characters, 800
head-foot colour, 801
- ranges, marine gastropods, 593
- Rangia cuneata, 337
- Rapaninae, 822
- Raphistomina, Ordovician, 92
- Rastodens, 744
operculum, Fg 15.104
radula, Fg 15.104
shell, Fg 15.104
- Rastodens puerilis, 744
external appearance, Fg 15.104

INDEX

- Rastodontidae, Fg 15.104, Tb 15.1, 741, 744
family treatment, 744
Rathouisia, 1065
distribution, 1064
Rathouisiidae, Fg 17.27, Pl 31, 1039, 1064
family treatment, 1064
habitat, 55
Simroth gland, 1049
ureter, 1045
Rathouisioidae, 1062
description, 1064
rats, Lord Howe Island, 114
Rattlesnake HMS, 7, 196, 919, 1038
rays, as cardiid predators, 329
razor fish, 265
razor shells, 340
Receptaculites, Devonian, 95
reciprocal copulation
Opisthobranchia, 588
Recluzia, 814
Recluzia rollandiana
shell, Fg 15.151
recruitment, Pinnidae, 267
rectal gland
Neogastropoda, 819
Scaphopoda, 435
Rectangularca, 257
Rectidentinae, 59
rectum, Cocculiniformia, 654
rectum/ventricle arrangement
Anomalodesmata, 401
red blood cells, taxodonts, 212
redox boundary layer, Fg 5.10
red-triangle slug
colour morphs, 1109
red-winged pearl shell, Pl 11
Reeve, Lovell A., 8, 162, 196, 337, 1038
refugia, Australian pulmonates, 1057
regeneration, Aplacophora, 148
regional mollusc faunas
inland waters, 59
regulatory detorsion
prosobranchs, 614
reinforcement sac, Neritidae, 697
rejection current
Yoldiidae, Fg 4.12
rejection tracts
Mytilidae, 251
Pinnidae, 266
rejection groove, Nuculidae, Fg 5.3
relationships
Anaspidea, 940
Caenogastropoda, 940
in deep water fauna, 80
Embletoniidae, 1015
estuarine fauna, 79
freshwater molluscs, 82
Gymnosomata, 940
Heterobranchia, 940
Littorinoidea, 940
marine and estuarine fauna, 77
Notaspidea, 940
Nudibranchia, 941
Philinoidea, 948
Retusidae, 950
Rhodopemorpha, 960
Ringiculidae, 940
Ringiculoidea, 946
Sacoglossa, 940
relaxation of specimens
Pulmonata, 1059
Relichna, 949, 950
Relichna murchisoni, 950
relocation, Mytiloidea, 206
renal gland, Caenogastropoda, 627
renal organ
Bivalvia, 203
Pulmonata, 1045
renal portal system
Gastropoda, 581
renal system
prosobranchs, 625
Renilla on sand plains, 38
Renilla koellikeri, 1008
renopericardial system
Rissooidea, 745
reproduction, 333, 407, 744, 745, 823, 850, 958, 1080, 1104, 1106
Achatinelloidea, Fg 17.40, 1080
Achatinoidea, Fg 17.47, Fg 17.49, 1087
Aeolidina, 1011
Amphiboloidea, Fg 17.29, Fg 17.30, 1067
Ampullarioidea, 706
Anaspidea, 934
Anomalodesmata, 401
Aplacophora, 148
Architectonicoidea, Fg 15.182, 859
Arionoidea, Fg 17.54, Fg 17.56, Fg 17.58
Avacoidea, Fg 17.52
Basommatophora, Fg 17.17, 1048
Bivalvia, 195, 214
Bulimuloidea, Fg 17.53
Caenogastropoda, 610
Camaenoidea, 1112
Carditoidea, 322
Carinarioidae, 804
Cephalaspidea, 934
Cephalopoda, 452, 468
Cerithioidea, Fg 15.86, Fg 15.88, Fg 15.94
Chaetodermatomorpha, 151
Cingulopsoidae, Fg 15.102, Fg 15.103
Cionelloidea, 1081
Cocculinoidea, 655
Coleoidea, Fg 11.22, 501
Conoidea, 847
Corbiculoidea, 353
Cyclophoroidea, Fg 15.78, 703
Cypraeoidea, Fg 15.131
Ellobioidea, Fg 17.37, 1076
Gastropoda, 586
Glacidorboidea, Fg 17.36, 1075
Gymnosomata, 986
Haminoeidea, 954
Helicoidea, Fg 17.71, Fg 17.72, 1113
Heterobranchia, Fg 15.179, Fg 15.182–15.185
Heterodonta, 303
kidney, role, 625
Lepetelloidea, 658
Limacoidea, Fg 17.59–17.65, 1102
Limapontiidae, 973, 974
Littorinoidea, Fg 15.100
Lucinoidea, 303
Lymnaeoidea, Fg 17.35, Fg 17.31–17.33
Macroidea, 337
Mollusca, 19
Muricoidea, Fg 15.155, 820
Myoidea, 362
Myoidea, 363
Nautiloidea (superfamily), Fg 12.11
Neogastropoda, Fg 15.155
Neomeniomorpha, 152
Neritoidea, 694
Neritopsina, Fg 15.73, Fg 15.75
Notaspidea, 934
Octopoda, Fg 11.22
Omaliogyroidea, Fg 15.185, 864
Onchidioidea, Fg 17.26
Opisthobranchia, Fg 16.18, 918, 932
Otinoidea, Fg 17.25
Palaeoheterodonta, 292
Partuloidea, Fg 17.45, 1085
Pholadoidea, 374
Pholadomyoidea, 406
Pleurotomarioidea, 665
Polygyroidea, Fg 17.68
Polyplacophora, Fg 3.11, 20, 172
Pomatopsioidea, Fg 15.112
prosobranchs, 631
Ptenoglossa, Fg 15.149, Fg 15.150
Pterotracheidae, 808
Pulmonata, Fg 17.2, Fg 17.17, Fg 17.18, Fg 17.39, 1037, 1048
Pupilloidea, Fg 17.44, 1082
Pyramidelloidea, 865
Rathouisioidae, Fg 17.27, Fg 17.28
Rhytidioidea, Fg 17.51, 1091
Ringiculoidea, 946
Rissoelloidea, Fg 15.184, 862
Rissooidea, Fg 15.108, Fg 15.110, Fg 15.115, 745
Sacoglossa, 961
Scaphopoda, Fg 10.9, 436, 437
Sepioidea, Fg 11.22
Siphonarioidea, 1067
strategies, 23
Streptaxoidea, 1090
Stylommatophora, Fg 17.39, 1080
Succinoidea, Fg 17.66, Fg 17.67
Systellommatophora, 1049
Thecosomata, 980
timing in bivalves, 24
Tonnoidea, Fg 15.143, 793
Trimusculoidea, Fg 17.38
Triphoroidea, Fg 15.149, Fg 15.150
Trochoidea, 672
Valvatoidea, Fg 15.179, 856
Velutinoidea, Fg 15.132, 786
Veneroidea, 356
reproductive cycles
Camaenidae, 1052
gametogenesis, 24
Gastropoda, 591
Pectinidae, 277
Pinnidae, 266
reproductive morphology
Gastropoda, 587
males, 23
Opisthobranchia, 588
Patellogastropoda, 587
Pulmonata, 589
Systellommatophora, 1049
Vetigastropoda, 587
reproductive primordia
Basommatophora, 1051
Stylommatophora, 1051
reproductive strategies, 29
Anomalodesmata, 402
Bivalvia, 217
Coleoidea, 470, 471
Corbiculidae, 354
estuarine bivalves, 218
estuarine molluscs, 41
freshwater bivalves, 218
Heterodonta, 303
marine bivalves, 218
Mytilidae, 218
switching in bivalves, 218
Teredinidae, 218
Xylophaginae, 218
reproductive system
Caenogastropoda, Fg 14.28
Opisthobranchia, Fg 14.30
prosobranchs, Fg 14.28
Pulmonata, Fg 14.32
Vetigastropoda, Fg 14.28
repugnatory glands, 918
Hydatinidae, Fg 16.7
Nudibranchia, 990
Opisthobranchia, 924
Phenacolepadidae, 700
resilifer
Bivalvia, 200
Mactridae, Fg 8.22
Mesodesmatidae, Fg 8.23
resilium
Anomalodesmata, Fg 9.1
Resolution, 6
resorption,
Coleoidea, 501
Stylommatophora, 1046
resorting current
Yoldiidae, Fg 4.12
resource partitioning
Neritidae, 698
respiration
adaptations on land, 580
Amphibolidae, 1046
Ancyliidae, 1046
apertural adaptations, 625
Aplacophora, 147
Architectonicidae, 862
Athoracophoridae, 1047
Basommatophora, 1046
Bivalvia, 211
Heterodonta, 303
intertidal species, 625
Lottiidae, 625
Mathildidae, 859
Mollusca, 17
Opisthobranchia, 915, 928
Palaeoheterodonta, 291
Planorbidae, 1046
Polyplacophora, 168
prosobranchs, 623, 624
Pulmonata, 1046
Rissoellidae, 862
Scaphopoda, 434
Siphonariidae, 1046
Stylommatophora, 1046
terrestrial Caenogastropoda, 580
terrestrial molluscs, Fg 1.64, 18, 625
terrestrial Neritopsina, 580
tracheopulmonates, 1047
Tridacnidae, 333
respiration rate
prosobranchs, 625
respiratory current
Scaphopoda, 434
respiratory flow
and pallial organs, 616
respiratory folds
Aplacophora, 146
Neomeniomorpha, 146
respiratory pigments
Bivalvia, 210
Pulmonata, 1047
respiratory system
Octopoda, Fg 11.18
Sepioidea, Fg 11.18
Reticulidia, 1001
retina
Pulmonata, Fg 17.15
Retispira
Carboniferous, 95
Devonian, 95
Permian, 97
Retizafra, shell, 827
retractor muscle scars, Fg 7.9, Fg 8.39
retractor muscles, Fg 4.9
Bivalvia, Fg 4.8
Dentaliida, 439
Dentaliidae, Fg 10.4
Pandoridae, 416
Petricolidae, Fg 8.39
Pharidae, Fg 8.26

- retrograde wave, Fg 15.4
- Retusa*, 926, 937, 949, 950, 974
- Retusa chrysoma*, 937
- Retusa obtusa*, 950
- Retusa pelyx*, Fg 16.28, 937
- external appearance, Fg 16.28
- shell, Fg 16.28
- Retusa truncatula*, 950
- Retusidae, Fg 16.28, 943
- family treatment, 949
- Retusophilina*, 951
- reverse estuaries, 40
- Reynellona*, 741
- Reynellona natalis*, 741
- shell, Fg 15.101
- Reynellonidae, 740
- Rhabdidae, 439
- Rhabditae, family treatment, 442
- Rhabdocanthus altum*
- Permian, Fg 1.99
- Rhabdoderma*, 151
- Rhabdoderma australe*
- external features, Fg 2.6
- Rhabdus*, 442
- Rhabdus rectius*, 435, 436, 439
- diet, 437
- feeding, 434
- Rhachistia*,
- Gondwanan origin, 1086
- radula, 1085
- Rhachistia bidwilli*, 1085
- Rhachistia histrio*, 1085
- external appearance, Fg 17.45
- pseudosigimurethry, 1085
- radula, Fg 17.45
- reproduction, 1085
- shell, Fg 17.45, 1085
- Rhacopoda, characters, 3
- Rhagada*, 81
- courtship, 1055
- Rhagada harti*
- shell, Fg 17.69, 1112
- Rhagadidae, 86
- Rhaphauls chrysalis*
- breathing tube, Fg 14.18
- rhinoglossate radula
- Triphoridae, 810
- Rhinoclama*, hinge teeth, 424
- Rhinoclavis*, 712
- locomotion and shape, 576
- shell modification, 572
- Rhinoclavis aspera*
- columellar folds, Fg 14.12
- external appearance, Fg 14.12
- Rhinoclavis fasciata*
- intertidal distribution, 43
- Rhinoclavis sinensis*, 712
- Rhinoclavis vertagus*
- intertidal distribution, 43
- shell, Fg 15.83
- Rhinoclavus*, osphradium, 577
- Rhinodiaphana*, 951
- rhinophores, 918, 999
- Aegiretidae, 995, 996
- Aeolidiidae, 1012
- Aeolidina, 1011
- Anaspidea, 932
- Arminidae, 1007
- Charcotiidae, 1008
- Corambidae, 990
- Dendrodorididae, 1000
- Dendronotina, 1001
- Doridomorphidae, 1008
- Dotidae, 1004
- Embletoniidae, 1015
- Eubranchidae, 1012
- Fionidae, 1017
- Flabellinidae, 1012
- Glaucidae, 1013
- Gymnodorididae, 995
- Hancockiidae, 1003
- Hexabanchidae, 997
- Lomanotidae, 1007
- Madrellidae, 1009
- Nautilus*, 468
- Notaspidea, 932
- Nudibranchia, 923, 932
- Onchidorididae, 992
- Opisthobranchia, Fg 16.17
- Phyllidiidae, 1000
- Phylliroidea, 1006
- Pinufiidae, 1010
- Sacoglossa, 922
- Scyllaeidae, 1005
- Tergipedidae, 1016
- Tethydidae, 1005
- Triophinae, 993
- Tritoniidae, Fg 16.17, 1002
- Vayssiéridae, 996
- Zephyrinidae, 1009
- Rhiostoma housei*
- breathing tube, Fg 14.18
- Rhipidoglossa, 620
- rhpidoglossate radula, Fg 1.14,
- 582, 620, 664
- Rhizoclonium*, 972, 974
- Rhodope*, Fg 16.43, 960, 961
- external appearance, Fg 16.43
- Rhodope veranyi*, 960, 961
- Rhodopemorpha, characters, 960
- Rhodopetala*, parental care, 637
- Rhodophyta, in diet of
- Hermæidae, 972
- Rhodopidae, Fg 16.43
- affinities, 1062
- characters, 960
- Rhombopteria*, Tb 1.6
- Rhombostoma*, 752
- Rhopalomenia*
- cuticle, 146
- development, 148
- Rhopodon kempseyensis*
- shell, Fg 17.55
- Rhynchidia*, as fossils, 695
- rhynchodeum
- Conidae, 852
- Conoidea, 846
- rhyncholite
- Nautilida, 493
- rhynchostome
- Conoidea, 846
- Melongenidae, 831
- rhynchoteuthion
- Ommastrephidae, 502, 532
- Rhynchotrochus macgillivrayi*,
- Pl 32
- Rhyssoplax*, Tertiary, 187
- Rhyssoplax calliozona*, Fg 3.38,
- Pl 8, 172, 185
- aesthetes, Fg 3.18
- eggs, 173
- habitat, 175
- Rhyssoplax diaphora*, Pl 8, 185
- Rhyssoplax exoptanda*, Pl 8
- eggs, 173
- habitat, 175
- Rhyssoplax olivaceus*, 185
- Rhyssoplax torriana*, 185
- Rhyssoplax tricostalis*, Pl 8, 185
- eggs, 173
- Rhytida*, affinities, 1093
- Rhytida greenwoodi*, 1058
- Rhytididae, Fg 1.65, Fg 17.8,
- Fg 17.10, Fg 17.20,
- Fg 17.51, Pl 31, Tb 1.5, 15,
- 86, 1091
- body form and carnivory, 1039
- family treatment, 1091
- fossils, 1058
- Gondwanan origins, 1057
- as predators, 1093, 1106
- Rhytidoidea, 1091
- description, 1091
- families, 1091
- Rhytidentalium kentuckyensis*, 443
- as fossils, 437
- Ribeiria*
- Ordovician, 93
- in Upper Cambrian, 92
- rice grain vacuoles, Fg 16.20
- Rictaxis*, 943, 944
- Riechian fluvifauna
- freshwater molluscs, 81
- Riechian Province, Fg 1.89
- Rimella*, 766
- Rimella cancellata*
- distribution, 766
- Rimula*, shell, 669
- Ringicula*, Fg 16.24, 943, 946
- external appearance, Fg 16.24
- organisation, Fg 16.1
- shell, Fg 16.24
- Ringiculida, 946
- Ringiculidae, Fg 16.24
- family treatment, 946
- Ringiculina*, 946
- Ringiculinopsis*, 946
- Ringiculoidea
- characters, 946
- mantle cavity, 946
- Ringiculopsis*, 946
- Ripalania*, 82, 729
- distribution, 82
- Risbecia*, 1000
- Rissoa*, 751
- development, 751
- prostate gland, 632
- as pyramidellid host, 867
- Rissoa membranacea*
- nurse eggs, 635
- Rissoa parva*, 614
- genital ducts, Fg 15.22
- Rissoa splendida*, 55
- cue for settlement, 54
- Rissoella*, 862
- affinities, 862
- egg capsules, 863
- external appearance, Fg 15.184
- subgenera, 864
- Rissoella diaphana*
- morphology, Fg 15.184
- Rissoella globosa*, shell, Fg 15.184
- Rissoella (Jeffreysiella)*
- distribution, 864
- radula, 864
- shell, 864
- Rissoella (Jeffreysiella) secunda*
- radula, Fg 15.184
- shell, Fg 15.184
- Rissoella micra*
- operculum, 863
- radula, Fg 15.184
- Rissoella (Rissoella)*
- distribution, 864
- shell, 864
- Rissoella (Zelaxitas)*
- distribution, 864
- shell, 864
- Rissoellidae, Fg 15.184, Tb 15.1,
- 862
- affinities, 862
- family treatment, 862
- relationships, 566, 606
- Rissoellina, 862
- Rissoelloidea, Tb 15.1
- description, 862
- Rissoidae, Fg 15.108, Tb 15.1,
- 749, 772
- family treatment, 749
- oviduct, 745
- shell ornamentation, 614
- Rissoina*, 632, 749, 751
- distribution, 751
- Jurassic, 97
- Rissoina chathamensis*, 749
- internal morphology, Fg 15.108
- Rissoina pulchella*, shell, Fg 15.108
- Rissooidea, Tb 15.1, 566, 606
- affinities, 745
- crystalline style, 621
- description, 745
- on land, 55
- plesiomorphies, 745
- Rissopsis*
- in Australia, 752
- distribution, 752
- Rivomarginella*
- in freshwater, 841
- Roboastrea*, 994
- radula, Fg 16.76
- Roburnella*, 941, 963, 964
- Roburnella wilsoni*, Fg 16.45,
- Pl 37, 964
- external appearance, Fg 16.45
- rock lobsters
- and *Octopus tetricus*, 549
- rocky shores
- commensalism, 32
- competition for food, 31
- ecological interactions, 30
- importance of molluscs, 32
- limpets, 643
- Lottiidae, 650
- predatory molluscs, 32
- rodents
- as camaenid predators, 1112
- Roebuck*, 6
- Roe's abalone, fishery, 73, 669
- Rondeletiola*, 511
- Rossia australis*, Fg 13.7, 511
- arm crown, Fg 13.7
- external appearance, Fg 13.6
- male tentacular club, Fg 13.7
- Rossia macrosoma*, 511, 514
- Rossia pacifica*, 511, 514
- diet, 514
- Rossia palpebrosa*, 511
- Rossiinae, 510
- Rossoceras*, endocones, 488
- Rostanga*, Fg 16.17, 934, 936, 938
- radula, 999
- rhinophores, Fg 16.17
- Rostanga arbutus*, Fg 16.11,
- Fg 16.17
- jaw plate, Fg 16.11
- rhinophores, Fg 16.17
- Rostanga australis*, Fg 16.17
- rhinophores, Fg 16.17
- Rostanga bassia*, Fg 16.17
- rhinophores, Fg 16.17
- Rostanga bifurcata*, Fg 16.17
- rhinophores, Fg 16.17
- Rostanga calumus*, Fg 16.17,
- Fg 16.82
- jaw plates, Fg 16.82
- radula, Fg 16.82
- rhinophores, Fg 16.17
- Rostanga muscula*, Fg 16.17
- rhinophores, Fg 16.17
- Rostangidae, 997
- Rostroconchia, 3, 223, 438
- adaptations to burrowing, 223
- Devonian, 95
- features, 5, 92
- in fossil record, 88

INDEX

- Ordovician, Fg 1.98, 93
origins, 92
radiation, 223
- Rotacharopa annabelli*
apical shell sculpture, Fg 17.55
shell sculpture, Fg 17.55
- Rotacharopa densilamellata*
shell, Fg 17.55
- Rotadiscinae, 87
- Rotifera, sperm dimorphism, 20
- Rowley Shoals, *Nautilus*, 494, 495
- Roxania*, 956, 959
Cretaceous, 956
distribution, 956
shell, 956
- Roxaniella*, 955
- Roybellia*
Norfolk Island, 1106
- Royella*, 712
- Royella sinon*
distribution, 712
- Ruditapes*
as ranellid prey, 800
- Rudman, William B., 920
- Ruedemannia*, Carboniferous, 95
- Rumphius, Georgius Everhardus, 161
- Rumtunucula*, 237
- Runcina*, 958
- Runcina australis*, Fg 16.37, 958
external appearance, Fg 16.37
- Runcina fijiensis*, 958
- Runcina katipoides*, Fg 16.13
alimentary tract, Fg 16.13
gizzard, Fg 16.13
gizzard plates, Fg 16.13
- Runcinella*, 958
- Runcinella zelandica*, 958
- Runcinida, 958
- Runcinidae, Fg 16.13, Fg 16.37
family treatment, 958
gizzard, Fg 16.13, 926
gizzard plates, Fg 16.13
gut, Fg 16.13
- Runcinoidea, 940
characters, 958
diet, 937
- Runnegaria*, Ordovician, Tb 1.6
- Rzehakia*, as fossils, 356
- Rzehakiidae, 356
- prey of whelks, 32
State fisheries, Fg 1.80
- Saccostrea cucullata*, 196, 272
fishery, 74
shell, Fg 6.15, 199
- Saccostrea echinata*, 272
fishery, 74, 75, 220
- Saccostrea glomerata*
affinities, 272
prodissoconch, Fg 4.21
- Sacella*
Tertiary, 99
- Sacoglossa
ancestral taxa, 940
characters, 961
classification, 962
diet, 937
egg masses, 935
as fluid feeders, 583
morphological diversity, 937
radiation, 940
relationships, 961
symbiotic plastids, 939
- Sagamicadulus*, 445
- Sagaminopteron*, 953, 954
- Sagaminopteron ornatum*, Fg 16.9,
Pl 33, 954
- Sagaminopteron psychedelicum*
external appearance, Fg 16.32
- Sagdidae
distribution, 1110
encrustation, 571
- Sagenotriphora ampulla*, radula,
Fg 15.149
- sailing, Terebridae, 850
- Sakuraeolis enosimensis*, Fg 16.19
egg masses, Fg 16.19
- Salaputium*, 327
diversity, 326
as fossils, 327
Tertiary, 99
- Salaputium fulvidus*, shell, Fg 8.14
- Salinator*, 1067
egg masses, 25
operculum, 1055
visceral commissure, 1067
water conservation, 1055
- Salinator cf. fragilis*, 1067
radula, Fg 17.29
- Salinator fragilis*, Fg 1.48, 937,
1067
distribution, 1067
egg mass, Fg 1.20
genitalia, Fg 17.29
in mangroves, 45
nerve ganglia, Fg 17.29
shell and operculum, Fg 17.29
- Salinator solida*, Fg 1.48, 1067
distribution, 1067
operculum, Fg 17.29
shell, Fg 17.29
sperm ultrastructure, Fg 17.19
- saline waters, *Coxiella*, 65
- salinisation
effects on Hyriidae, 61
- salinity
in estuaries, 40
estuarine molluscs, 40
- salinity tolerance, Lolliginidae, 519
- saliva, function in Coleoidea, 500
- salivary glands
Caenogastropoda, 620
Coleoidea, 500
Conidae, 847
Conoidea, 847
Patellogastropoda, 620
prosobranchs, 620
Pulmonata, 1043
Turridae, 847
Vetigastropoda, 620
- salivary toxins, Coleoidea, 500
- Salmacina dysteri*, 996
- Salpa tilesii*
as host to *Ocythoe*, 552
- salps,
and *Ocythoe*, 552
as carinariid prey, 804, 806
- Salsipotens*, 686
- salt lakes and conservation, 112
- Saltocuna*, 325
- Samacar*, 254
habitat, 256
- Samarang HMS*, 7
- Samarangia*, 360
sand coating, 301
sand on shell, 356
- Samarangia quadrangularis*
habitat, 360
- Samarangiinae, 356, 360
- sampling methodology, 104
- sand bonding
Anomalodesmata, 398
Clavagellidae, 398
function, 398
gland secretion, 398
Lyonsiidae, 398
Parilimyidae, 398
Periplomatidae, 398
Verticordiidae, 398
- sand collar, 790
- sand creepers, 707
- sand dollars, 38
- sand plains
physical environment, 38
- Sandalops melancholicus*
external appearance, Fg 13.28
- Sanguinolaria nuttallii*
feeding, 304
- Sanguinolariidae, 345
- Sanguinolites*, Tb 1.6
Devonian, Tb 1.6
- Sanhaliotis*, 667
- Sanmartinoceras*, Cretaceous, 99
- Sanmartinoceras fontinale*
Cretaceous, Fg 1.100
- Sansonia*, 740
- Sansonia andamanica*, 740
- Sansonia kirkpatricki*, 740
shell, Fg 15.101
- Sapha amicorum*, 951
- Sarcophytum*, as ovulid host, 786
- Sarepta*, 240
diversity, 240
- Sareptidae, Fg 5.7, 239
family treatment, 240
- Sargassum*, 715
- Sassia*, 800
as fossils, 793, 800
head-foot colour, 801
radula, 800
Tertiary, 99
- Sassia (Austrotriton)*
development, 800
- Sassia remensa*
protoconch, Fg 15.142
- Sassia subdistorta*
egg mass, Fg 1.20
- Saturnia*, 239
- Saturniidae, 239
- saucer scallop, 277
- Sawkinsia*, as fossils, 336
- Saxicava*, 370
- Saxicavella*, 370
epifaunal, 370
mantle fusion, 370
- Saxidomus*
antifeedants, 358
- distribution, 360
habitat, 360
- Scaeoleda*
diversity, 239
- Scaevargus*, hectocotylus, 549
- Scalaetrochus*, Devonian, 95
- Scalenostoma*, diversity, 817
- scales, Lepidoteuthidae, 526
- Scaliola*, 732, 733
affinities, 733
encrustation of shell, 571
external appearance, Fg 15.97,
732
as fossils, 733
radula, Fg 15.97
- Scaliolidae
affinities, 733
in Australia, Fg 15.97, Tb 15.1
euspermatozoa, 708
family treatment, 732
- scallop dredging
effect on environment, 115
- scallop fisheries, 73, 74, 249, 275
annual catches, Tb 1.3
Australian catch, 220
commercial utilisation, 39
economic importance, 74
in seagrass, 39
status of fisheries, 74
- Scaphander*, 586, 948, 949
- Scaphander illecebrosus*, 949
- Scaphander lignarius*, Fg 16.4,
Fg 16.10, Fg 16.14, 949
external appearance, Fg 16.4
gizzard plates, Fg 16.14
radular teeth, Fg 16.10
shell, Fg 16.4
- Scaphander otagoensis*, 949
- Scaphandridae, Fg 16.4, Fg 16.10,
Fg 16.14, 932
evolution of body form, Fg 16.4
evolution of shell, Fg 16.4
gizzard plates, Fg 16.14
radula, Fg 16.10
- Scaphanidia*, as fossils, 695
- Scapharca*, 254
burrowing, 254
habitat, 256
ligament, 254
shell, 254
- Scaphella*, radula, 842
- Scaphella (Aurinia)*
as fossils, 835
- Scaphites*, Cretaceous, 99
- scaphoconch, 787
- Capulidae, 774
echinospira larva, Fg 15.30, 638
- Scaphopoda, Fg 10.16, Fg 10.18
age of class, 437
broadcast spawning, 25
characters, 5
circulatory system, 434
classification, 438
direct development, 22
ecology, 437
economic significance, 437
ect-aquasperm, 20
embryology and development,
436
excretion, 435
external appearance, shell, 432
feeding and digestion, 16, 433
in fossil record, 88
fossil record and phylogeny, 437
definition and description, 431
general features, 12
history of discovery, 431
larval development, 23
morphology and physiology, 432
musculature and locomotion, 433
natural history, 437
nervous system, 435

- as ovulid prey, 836
 Pulsellidae, 444
 reproduction, 436
 respiration, 434
 sense organs, 435
 stenocalymma larva, 436
 suborder Entalimorpha, 444
Scaphula, 253
Scelidionarca, 257
Sceptrites, 491
Schilderia, 780
Schistosoma, 746, 1072
 and Potamiopsidae, 756
Schistosoma haematobia
 economic importance, 68
Schistosoma japonica
 economic importance, 68
Schistosoma mansoni, 70, 1072
 economic importance, 68
Schistosoma mekongi, 70
 Schistosomatidae, 68
 schistosome dermatitis, 721, 1056
 schistosome vector
Austropelea tomentosa, 1056
 schistosomes
 dermatosis, 68
 economic importance, 66
 life cycle, Fg 1.76
 as parasites of Calyptraeidae, 774
 schistosomiasis, 1056
Schizmotis, 667
 as fossils, 669
Schizobranchea, 987
Schizochiton, 172, 183
Schizochiton brandtii, Fg 3.34
Schizochiton incisus, 184
Schizochitonidae, Fg 3.35,
 Fg 3.36, Pl 9, 180
 external appearance, Fg 3.35
 family treatment, 183
 genera, 176
 ventilation, 169
 schizodont system, Fg 4.6
Schizodus, Tb 1.6
 Devonian, Tb 1.6
 Permian, 97
 Schizoplacinae, 181
Schizoplax brandtii, 181
 Schneider, 452
 Cephalopoda, 452
 schooling
 Chiroteuthidae, 537
 Histiotteuthidae, 529
 Lepidoteuthidae, 527
 Loliginidae, Pl 18
 Ommastrephidae, 532
 Onychoteuthidae, 524
 Thysanoteuthidae, 533
Scintilla, shell, 318
Scintilla strangei
 external appearance, Fg 8.8
Sciponoceras, Cretaceous, 99
Scissuradentalium, 432
Scissurella, 666
Scissurella crispata
 radula, Fg 15.52
 Scissurellidae
 Australian fauna, Fg 15.52,
 Tb 15.1, 664, 666
 diversity, 666
 family treatment, 666
 pallial organs, 615
 Scissurellinae, 666
 Scissurelloidea, 664
 features, 610
Scissurona, 666
 Scleractinia
 as prey of Nudibranchia, 938
Scleronephthya, Pl 7
 prey, *Epimenia australis*, 156
Scrobicularia, 344
 affinities, 343
Scrobicularia plana
 external appearance, Fg 8.29
 sculpture, 241, 289, 494
 Anomalodesmata, 397
 Carditoidea, 322
 Dentaliida, 439
 Patellogastropoda, 643
 Polyplacophora, Fg 3.3
 Ptenoglossa, Fg 15.150
 Pulmonata, Fg 17.3
 Triphoroidea, Fg 15.150
 sculpture, nuclear
 Arionoidea, Fg 17.55
 Charopidae, Fg 17.55
Scurriopsis, Palaeozoic, 645
Scutellastra, 641, 645, 646
 in Australia, 645
 characters, 645, 646
 distribution, 644, 646
 Miocene, 644
 radula, Fg 15.34
 shell ultrastructure, 640
Scutellastra chapmani, 642, 646
 endemic, 646
 shell, Fg 15.35
Scutellastra flexuosa, 646
 distribution, 646
 endemic, 646
Scutellastra kermadecensis, 645
Scutellastra laticostata, 642, 646
 endemic, 646
Scutellastra longicosta
 radula, Fg 1.14
Scutellastra peronii, shell, Fg 15.35
Scutellastra peronii, endemic, 646
Scutellastra tabularis, 645
 Scutopoda, 2
Scutopus, 150
 musculature, 150
Scutus antipodes, shell, 671
Scyllaea, 1005
Scyllaea pelagica, Fg 16.91
 external appearance, Fg 16.91
 radula, Fg 16.91
 Scyllaeidae, Fg 16.91
 family treatment, 1004
 sea anemones
 as aeolidiid prey, 1012
 sea ears, 667
 sea hares, Pl 34, 975
 sea level changes
 effects on fauna, 77, 79
 sea pansies, 38
 sea slugs, 915
 sea-angels, 986
 seabirds
 as loliginid predators, 519
 sea-butterflies, 980
 seagrass
Amphibolis, 39
 direct consumers, 38
 effect on current, 39
 epifauna, 39
 Heterozostera, 39
 importance for molluscs, 38
 nursery role, 39
 physical environment, 38
Posidonia, 39
 role in food chain, 38
 as a substratum, 38
 substratum for limpets, 644
 seagrass beds, 38
 seals
 as loliginid predators, 519
 as sepiid predators, 508
 secondary gills, 1037
 Ancyliidae, 18, 1046
 Gastropoda, 17
 Nudibranchia, Fg 1.15
 Opisthobranchia, 18, 579
Patella, 579
 Patellogastropoda, 579, 640
 Planorbidae, 18, 1046
 Siphonariidae, 1046
 secondary hinge teeth
 Cleidothaeridae, 419
 Cuspidarioidea, 398
 Pandoroidea, 398, 415
 Parilimyidae, 406
 Pholadomyoidea, 406
 Poromyidae, 422
 Poromyoidea, 398
 secondary ligament, 406
 Anomalodesmata, Fg 9.1, 398
 Myochamidae, 418
 Pandoridae, 415
 Pandoroidea, 415
 Periplomatidae, 410
 Verticordiidae, 420
 secondary ureter
 Pulmonata on land, 1046
 sedimentary basins, Fg 1.95
Seguenzia, 692
 shell, Fg 15.70
Seguenzia megaloncha
 radula, Fg 15.70
 Seguenziidae, Fg 15.70, Tb 15.1,
 682
 Australian genera, 692
 family treatment, 692
 Seguenzioidea, Tb 15.1, 664
 affinities, 692
 description, 692
 fertilisation, 631
 relationship, Trochoidea, 610
Seila, distribution, 811
Seila terebelloides
 radula, Fg 15.150
Seilarex, dextral shell, 809
 selenizone
Pleurotomaria westralis, 665
 Pleurotomariidae, 665
 Pleurotomarioidea, 664
Selenoteuthis, 520
 vertical migration, 520
 self-fertilisation
 Lymnaeidae, 1071
 Testacellidae, 1108
Semelangulus, 344
Semelartemis, 360
Semele, 344
Semele amabilis
 size, 344
Semele casta
 distribution, 344
 shell, Fg 8.29
Semelidae, Fg 8.29, 340, 343
 family treatment, 344
 as prey of fishes, 344
 semelparity, 29
 Cephalopoda, 51
 Coleoidea, 470, 502
 Cranchiidae, 540
 Galeommatoidea, 217
 Modulidae, 731
 Octopodidae, 549
 Ommastrephidae, 532
 Onychoteuthidae, 524
 Opisthobranchia, 29
 Sphaeriidae, 217, 218
Semicassis, 795–796
 distribution, 796
 egg mass, 793
 habitat, 794
 larval dispersal, 796
Semicassis adcocki, Pl 27
Semicassis bisulcata
 distribution, 796
Semicassis labiata
 distribution, 796
 feeding, 796
Semicassis pyrum
 distribution, 796
 as fossils, 797
 shell, Fg 15.137
 seminal receptacle, Fg 15.22
 Caenogastropoda, 632
Semipallium, 278
Semiretusa, 949
 semi-slugs, Pl 32
 Fissurellidae, 614
 Lamellariidae, 614
 Naticidae, 614
 prosobranchs, 614
 Pulmonata, 1039
Titiscania, 614
 Trochoidea, 614
Semisulcospira, 70
Semivertagus capillatus
 as fossils, 712
Semotrachia, 81
Semotrachia esau
 genitalia, Fg 17.18
 sense organs
 Aglajidae, 932
 Anomalodesmata, Fg 9.3, 401
 Aplacophora, 147
 Bivalvia, Fg 4.18, 212
 Cephalopoda, Fg 11.20,
 Fg 11.21, 451, 465
 Gastropoda, 18, 576
 Heterodonta, 303
 Laternulidae, Fg 9.3
 Mollusca, 18
 Octopoda, Fg 11.20
 Octopodidae, Fg 11.20
 Opisthobranchia, 929
 Palaeoheterodonta, 291
 Philinidae, 932
 Polyplacophora, 18, 170
 Poromyidae, Fg 9.3
 prosobranchs, 629
 Pulmonata, 1047, 1048
 Scaphopoda, 435
 Sepioidea, Fg 11.20
 sensory bursicles
 Seguenziidae, 693
 sensory filaments
 Vampyroteuthidae, 454
 sensory organs, Tridacnidae, 333
 sensory papillae, Fg 15.20
 prosobranchs, 630
 Trochidae, Fg 15.20
 Vetigastropoda, Fg 15.20
 sensory reception
 Bivalvia, 219
 Gastropoda, 576
 Patellogastropoda, 640
 sensory structures
 Opisthobranchia, Fg 16.17
 sensory tentacles
 Palaeoheterodonta, 291
Separitista, 775
Sepia, 452, 471, 475, 487, 499,
 505, 507, 1017
 behaviour, Fg 11.27
 camouflage, 454
 cardiac parameters, 462
 cornea, 452
 courtship, 473
 ctenidial structure, Fg 11.18
 digestive enzymes, 500
 dymanic patterns, Fg 11.27
 external appearance, Fg 11.10
 fertilisation, 469
 fin shape, Fg 11.10
 food absorption, 500
 gas exchange, Fg 11.18

INDEX

- hatching gland, 470
- multiple spawning, 471
- nervous system, Fg 1.16
- oxygen uptake, 456, 465
- prey capture, 458, 474
- proteolytic enzymes, 459
- salivary toxins, 500
- shell, 453
- stellate ganglia, 466
- Sepia andreana*, fishery, 508
- Sepia apama*, Fg 1.3, Pl 17, 473
 - beak, Fg 11.25
 - courtship, Fg 11.26
 - distribution, 508
 - external appearance, Fg 11.1, Fg 13.2
 - growth, 508
 - mantle, 505
 - mortality, 508
 - radula, Fg 13.3
 - shell, Fg 13.3
- Sepia baxteri*
 - distribution, 509
- Sepia bilineata*, 499
- Sepia boscii*, 499
 - nomen nudum, 549
- Sepia braggi*
 - distribution, 508
 - external appearance, Fg 13.2
 - mantle, 505
 - shell, Fg 13.3
- Sepia brevimana*, fishery, 508
- Sepia chirorema*, distribution, 508
- Sepia cottoni*, distribution, 508, 509
- Sepia cultrata*
 - depths, 508
 - distribution, 508
- Sepia dannevi*, distribution, 508
- Sepia elegans*
 - depths, 508
 - fishery, 508
- Sepia elliptica*
 - diet, 508
 - distribution, 508
- Sepia esculenta*, fishery, 508
- Sepia hedleyi*, distribution, 508
- Sepia hierredda*, fishery, 508
- Sepia irvingi*, distribution, 509
- Sepia latimanus*, Pl 17, 508
 - distribution, 508
 - fishery, 508
- Sepia lorigera*, fishery, 508
- Sepia lycidas*, fishery, 508
- Sepia madokai*, 508
- Sepia mestus*, distribution, 509
- Sepia minima*, 499
- Sepia mira*, distribution, 509
- Sepia novaehollandiae*
 - distribution, 508
- Sepia officinalis*, 505, 507, 508
 - alimentary tract, Fg 11.14
 - camouflage, Fg 11.5
 - diet, 508
 - in dolphin diet, 508
 - embryology, Fg 11.23
 - fishery, 508
 - lateral line system, 468
 - life span, 508
 - prey capture, 502
 - sexual maturity, 507
 - spawning control system, 471
- Sepia opipara*
 - distribution, 508, 509
- Sepia orbignyana*
 - depths, 508
 - fishery, 508
- Sepia papuensis*, distribution, 508
- Sepia peroni*, 499
- Sepia peronii*
 - nomen nudum, 549
- Sepia pharaonis*
 - diet, 508
 - distribution, 508
 - fishery, 508
 - sexual maturity, 507
- Sepia plangon*
 - distribution, 509
- Sepia reesi*, distribution, 509
- Sepia rex*
 - distribution, 508
 - mantle, 505
- Sepia rozella*, distribution, 509
- Sepia smithi*
 - diet, 508
 - distribution, 508, 509
- Sepia varietas*, 499
- Sepia vercoi*, distribution, 509
- Sepia whitleyana*, distribution, 509
- Sepiidae, 509
- Sepiariidae, Fg 13.4, Fg 13.5, Pl 18, 510
 - family treatment, 509
- Sepiariidae*, 509, 510
- Sepiariidae auritum*, 509, 510
- Sepiariidae austrinum*, 509, 510
 - burrowing, 510
 - external appearance, Fg 13.4
- Sepiariidae kochi*, Pl 18, 509, 510
 - radula, Fg 13.4, 510
- Sepiella*, 505, 507
- Sepiella inermis*, fishery, 508
- Sepiella japonica*, fishery, 508
- Sepiella maindroni*, fishery, 508
- Sepiella weberi*, distribution, 508
 - external appearance, Fg 13.2
 - shell, Fg 13.3
- Sepietta*, 511, 514
- Sepietta oweniana*, 514
- Sepiida, 452
- Sepiidae, Fg 1.3, Fg 1.16, Fg 11.1, Fg 11.5, Fg 11.10, Fg 11.14, Fg 11.18, Fg 11.23, Fg 13.2, Fg 13.3, Fgs 11.25–11.27, Pl 17
 - courtship, 22
 - family treatment, 505
 - first descriptions, 499
 - fisheries, 74
 - human consumption, 508
 - male combat, 22
- Sepioidea
 - description, 504
- Sepioida*, 509, 511, 514
 - external appearance, Fg 11.10, Fg 13.6
 - fecundity, 469
 - fin shape, Fg 11.10
 - luminescent organs, 511
 - statocyst, Fg 11.21
- Sepioida birostrata*, 514
- Sepioida lineolata*, 499, 509
- Sepioida robusta*, 511
- Sepioida rondeletii*, 511, 514
- Sepioida tasmanica*, 511
- Sepiolida, 452
- Sepiolidae, Fg 11.20, Fg 11.21, Fg 11.27, Fg 13.6, Fg 13.7, 511
 - family treatment, 510
 - ink and luminescence, 51
 - subfamilies, 510
- Sepiolina*, 511
 - light organs, 511
- Sepiolina nipponensis*, 511
 - arm crown, Fg 13.7
 - external appearance, Fg 13.6
 - hectocotylus, Fg 13.7
 - male tentacular club, Fg 13.7
- Sepiolinae, 510, 511
- Sepioloidea*, 509, 510
- Sepioloidea lineolata*, Pl 18, 509, 510
 - diet, 510
 - external appearance, Fg 13.4, 509
 - funnel locking apparatus, Fg 13.5
- Sepioloidea pacifica*, 510
 - mantle cavity, 510
- sepioid, 505
- Sepioteuthis*, 517
 - dymantic patterns, Fg 11.27
 - egg size, 469
 - shell, 517
- Sepioteuthis australis*, 499, 517, 519
 - communal egg mass, 519
 - egg capsule, 519
 - endemism, 520
 - external appearance, Fg 11.1, Fg 13.9
 - hectocotylus, Fg 13.9
- Sepioteuthis bilineata*, 517, 519
- Sepioteuthis lessoniana*, 517
 - age at maturity, 519
 - age determination, 519
 - captive breeding, 519
 - courtship, 519
 - distribution, 520
 - egg capsule, 519
 - egg laying, Pl 18
 - external appearance, Fg 13.9
 - hectocotylus, Fg 13.9
 - mating behaviour, 519
 - radula, Fg 13.9, 519
- Sepioteuthis sepioidea*
 - captive breeding, 519
 - egg capsule, 519
 - pairing, 517
- septa
 - Nautiloidea, 485
- Septa parthenopaeum*
 - larval dispersal, 637
- Septa rubicunda*, 6
- Septa spengleri*, 6
- septal gland
 - Coleoidea, 501
- septal muscles
 - Anomalodesmata, 399
 - Cuspidariidae, 399
 - Poromyidae, 399
- septal necks, 494
 - Discosorida, Fg 12.7
 - Nautiloidea, Fg 12.3
 - Nautilus*, 494
- septal retractor muscles
 - Cuspidariidae, 424
 - Poromyidae, 422
- Septaria*, distribution, 695
- septation, Ancyliidae, 1072
- Septentrioploma*, 410
- septibranch bivalves
 - feeding, 16
- Septibranchia, 225
- Septifer*, gills, 251
- Septifer bilocularis*, 196, 250
- septum, 494
 - Ancyliidae, 1071
 - Cuspidariidae, 400, 424
 - Discosorida, Fg 12.7
 - Anomalodesmata, 400, 422, 424
 - Nautiloidea, Fg 12.3
 - Nautiloidea, 485, 486
 - Oncocorida, Fg 12.4
 - Poromyidae, 400, 422
- septum formation
 - Caecidae, Fg 15.117
 - Rissooidea, Fg 15.117
- Sequenzia polita*, 692
- Sermylasma*, 82, 729
 - distribution, 82
- serotonin
 - Bivalvia, 210
- Serpula*, 779
- Serpulorbis*, 779, 780
 - encrustation of shell, 571
 - pallial cavity, Fg 15.129
 - web-feeding, 584
- Serpulorbis siphon*, Pl 24, 780
 - as fossils, 780
 - shell, 778
- Serpulorbis squamigerus*
 - mantle cavity, Fg 15.129
- Serpulospira*, Devonian, 95
- Serracorbula*, 366
 - shell, 366
- Serradonta*, 648
- Serrata*, 841
- Sesarma*, 45
- Setaliris*, 421
- Setomedeia janae*, shell, Fg 17.55
- Setomedeia monteithi*
 - shell sculpture, Fg 17.55
- settlement
 - bivalve larvae, 217
 - Cleidothaeridae, 420
 - cues, Bivalvia, 219
 - cues, veliger, 638
- settlement behaviour
 - Hiattellidae, 371
- sex determination
 - Bivalvia, 215
 - Eulimidae, 817
- sex ratio
 - Bivalvia, 214
 - Calyptraeidae, 774
- sex reversal
 - Caenogastropoda, 633
 - Calyptraeidae, 587, 633
 - Capulidae, 587, 633
 - Epitoniidae, 587
 - Eulimidae, 633
 - Hipponicidae, 587
 - Janthinidae, 587
 - Ostreidae, 270
 - timing, 633
- sexual dimorphism
 - Argonautidae, Fg 13.38, 552
 - Astartidae, 328
 - bivalve shell, 198
 - Bursidae, 793
 - Carditidae, 198
 - Cephalopoda, 452, 468
 - Eulimidae, 817
 - Ficidae, 797
 - Heterodonta, 303
 - Loliginidae, 517
 - Lycoteuthidae, 520
 - Nautiloidea, 454
 - Ocythoidae, Fg 13.37, 552
 - Oegopsida, 520
 - Tremoctopodidae, Fg 13.36, 551
 - Tricoliinae, 677
 - Unionidae, 198
- sexual expression
 - Bivalvia, 215
 - shell polymorphism, 215
- sexual maturity
 - Lottiidae, 642
 - Patelloidea, 642
 - Polyplacophora, 173
- Seymour Island
 - fossil Epitoniidae, 816
- shadow reflex, Bivalvia, 219
- Shark Bay, bivalves, 43
- Sheldonella*, 257
- Sheldonella repenta*, 258
- Sheldonella venustopsis*, 258

- shell
- Acanthochitonidae, Fg 3.41
- Achatinellidae, Fg 17.40, 1080
- Achatinelloidea, Fg 17.40, 1080
- Achatinidae, Fg 17.49, 1089
- Achatinoidea, Fgs 17.46–17.49, 1087
- Acididae, 816
- Acmaeidae, Fg 15.37, 648
- Acteonidae, Fg 16.21, 922, 943
- Addisoniidae, Fg 15.45
- Admetinae, 845
- Aglajidae, Fg 16.31, 928, 952
- Akeridae, Fg 16.56, 975
- Amathinidae, Fg 15.187, 868
- Amblemidae, 296
- Amphibolidae, Fg 17.29, Fg 17.30, 1067
- Amphiboloidea, Fg 17.29, Fg 17.30, 1067
- Ampullariidae, Fg 15.81, 706
- Ampullospirinae, 790
- Anabathridae, Fg 15.106
- Anaspidea, 974
- Ancillinae, Fg 15.165, 835
- Ancylidae, Fg 17.32, 1039, 1071
- Angariinae, Fg 15.56, 674
- Anomalodesmata, Fgs 9.7–9.11, Fgs 9.13–9.18, 397
- Anomiidae, Fg 6.20, 280
- Anomioidea, Fg 6.20, Fg 6.21, 280
- aperture dimensions, 614
- Apysidae, 976
- Architectonicidae, Fg 15.183, 861
- Architectonicoidea, Fg 15.182, Fg 15.183, 858
- Arcidae, Fg 6.2, 254
- Arcoidea, Fgs 6.2–6.4, 253
- Articoidea, Fg 8.33, 348
- Argonautidae, 552
- Arionidae, 1100
- Arionoidea, Fg 17.54, Fg 17.55
- Assimineidae, Fg 15.113, 756
- Astartidae, 328
- asymmetry, 566
- Athletinae, Fg 15.164
- Athoracophoridae, 1109
- Atlantidae, Fg 15.145, 804, 805
- Barleeidae, Fg 15.105, 746
- Basommatophora, Fg 17.29, 1067
- Bathysciadiidae, Fg 15.43, 656
- Batillariidae, Fg 15.90, 720
- Bithyniidae, Fg 15.116, 759
- Bittiinae, Fg 15.85, 710
- Bivalvia, Fg 4.1, Fg 4.2, 195–196, 198
- Bradybaenidae, Fg 17.72, 1115
- Buccinidae, Fg 15.159, 825
- Buccininae, Fg 15.159
- Bulimulidae, Fg 17.53
- Bulimuloidea, Fg 17.53
- Bullactidae, 955
- Bullidae, 957
- Bullinidae, Fg 16.22, 922, 944
- Bulloidea, 957
- Bursidae, Fg 15.136, 794
- Busyconinae, 832
- Cadulus similimus*, Fg 10.21
- Caecidae, Fg 15.117, 761
- Calliostomatinae, Fg 15.65, 686
- Calyptraeidae, Fg 15.126, 773
- Calyptraeoidea, Fg 15.126, 772
- Camaenidae, Fg 14.4, Fg 17.69, 1112
- Camaenoidea, 1112
- Campanilidae, Fg 15.98, 735
- Campaniloidea, Fg 15.98, 734
- Cancellariidae, Fg 15.172, 845
- Cancellariinae, 845
- Capulidae, Fg 15.127, 774
- Capuloidea, Fg 15.127
- Cardiidae, Fg 4.2, Fg 8.15, 328
- Cardiliidae, Fg 8.24, 340
- Cardioidea, Fg 8.15, Fg 8.17
- Carditidae, Fg 8.12, 322
- Carditoidea, Fg 8.12, Fg 8.13, 322
- Carinariidae, Fg 15.146, 806
- Carinarioidea, Fg 15.145, Fg 15.146, 804
- Cassidae, Fg 15.137, 794
- Cavoliniidae, Fg 16.62, 982
- Cephalaspidea, 943
- Cephalopoda, 451, 453
- Cerithiidae, Fg 15.83, Fg 15.85, 707, 710, 711
- Cerithinae, 709
- Cerithioidea, Fg 15.83, Fg 15.85, Fg 15.86, Fgs 15.87–15.92, Fgs 15.94–15.97, 707
- Cerithiopsidae, Fg 15.150, 811
- Chamidae, Fg 8.1, 307, 308
- Chamoidea, Fg 8.1, 301
- Charopidae, Fg 14.4, Fg 17.55
- Chitonidae, Fgs 3.38–3.40
- Choristellidae, Fg 15.45, 664
- Cimbrinae, Fg 15.164
- Cingulopsidae, Fg 15.102, 741
- Cingulopsoidea, Fgs 15.102–15.104
- Cionellidae, Fg 17.41, 1081
- Cionelloidea, Fg 17.41, 1081
- Cirrata, 453
- Clavagellidae, Fg 4.2, Fg 9.11, 397, 413
- Clavagelloidea, 412
- Cleidothaeridae, Fg 9.15, 397, 419
- Clementiinae, 360
- Cocculinellidae, Fg 15.45, 663
- Cocculinidae, Fg 15.42, 656
- Cocculinoidea, 655
- Coleoidea, 451, 453, 500
- Columbariinae, Fg 15.158, 825
- Columbellidae, Fg 15.160, 827
- Columbellinae, Fg 15.160
- Condyllocardiidae, Fg 8.13, 324
- Conidae, Fg 15.177, 846, 852
- Conoidea, 846
- Corbiculidae, Fg 8.35, 353
- Corbiculoidea, Fg 8.35, Fg 8.36, 352
- Corbulidae, Fg 8.42, 362, 366
- Corillidae, Fg 17.68, 1110
- Corniostridae, Fg 15.179, 856
- Costellariidae, Fg 15.171, 843
- Crassatellidae, Fg 8.14, 326
- Crassatelloidea, Fg 8.14, 306, 325
- Crassostreinae, 272
- Cryptoplacidae, Fg 3.42
- Cucullacidae, Fg 6.3, 256
- Cuspidariidae, Fg 4.2, Fg 9.18, 424
- Cyamiidae, Fg 8.9, 318, 319
- Cyamioidae, Fgs 8.9–8.11, 318
- Cyclindrobullidae, Fg 16.25
- Cyclophoridae, Fg 15.78, 704
- Cyclophoroidea, Fg 15.78, Fg 15.80, 703
- Cylichna alba*, Fg 16.4
- Cylichnidae, Fg 16.27, 948
- Cylindrobulloidea, 947
- Cylindromitrinae, Fg 15.169
- Cylleninae, Fg 15.161
- Cypraeidae, Fg 15.130, 780, 782
- Cypraeoidea, Fg 15.130, Fg 15.131, 780
- Cystiscinae, Fg 15.167
- Cystopeltidae, 1106
- Dentaliida, 439
- Dentaliidae, Fg 10.1, Fg 10.13, Fg 10.14
- development in Bivalvia, 216
- Dialidae, Fg 15.86, 707, 712
- Diaphanidae, Fg 16.26, 947
- Diastomatidae, Fg 15.95, 729
- Dimyidae, Fg 6.17, 274
- Diplommatinidae, Fg 15.80, 705
- Dischides prionotus, 447
- Donacidae, Fg 4.2, Fg 8.32, 346, 347
- Dorsaninae, 830
- Dosiniinae, 358
- Eatoniellidae, Fg 15.103, 743
- Elachisinidae, Fg 15.115, 758
- Ellesmerocerida, 487
- Ellobiidae, Fg 17.37, 1076, 1078
- Ellobioidea, Fg 17.37, 1076
- Emblandidae, Fg 15.107, 749
- Endocerida, 487
- Enidae, Fg 17.45, 1085
- Entalina, Fg 10.19
- Entalinidae, Fg 10.19
- Epigridae, Fg 15.109, 751
- Epitoniidae, Fg 14.4, Fg 15.152, 571, 814
- Eratoinae, 787
- Eucyclinae, Fg 15.61, 680
- Eulimidae, Fg 15.154, 817
- Eulimoidea, Fg 15.154
- Eupulmonata, 1076
- evolution, Aplacophora, 146
- Fasciolariidae, Fg 15.163, 832
- Ferrussaciidae, Fg 17.46, 1087
- Ficidae, Fg 15.138, 797
- Fimbriidae, Fg 8.4, 313
- Fissurellidae, Fg 15.54, 669
- formation, 13
- Fraginae, 331
- Fulgorariinae, Fg 15.164
- Fustiariidae, Fg 10.15
- Gabrieloninae, Fg 15.58, 676
- Gadilinae, Fg 10.21
- Gafrariinae, 358
- Galeommatidae, Fg 8.8, 316
- Galeommatoidea, Fg 8.8, 301, 316
- Gastrochaenidae, Fg 8.43, 367, 368
- Gastrochaenoidea, Fg 8.43
- Gastropoda, Fg 14.12, 569, 571
- Gastropoteridae, 952
- Gazini, 682
- Glacidorbidae, Fg 17.36, 1075
- Glacidorboidea, Fg 17.36, 1075
- Glaucanomia, Fg 8.40, 362
- Glossidae, Fg 8.34, 351
- Glossoidae, Fg 8.34, 301, 351
- Glycymerididae, Fg 6.6, 259
- Gryphaeidae, Fg 6.14, 269
- Halitidae, Fg 14.4, Fg 15.53, 664, 667
- Halistylinae, Fg 15.67, 688
- Haloceratidae, Fg 15.125, 772
- Haminoeidae, Fg 16.33, 954
- Haminoeidea, 954
- Harpidae, Fg 15.166, 837
- Harpinae, Fg 15.166, 837
- Helicarionidae, Fg 17.63, 1105
- Helicidae, 1113
- Helicinidae, Fg 15.77, 702
- Helicodiscidae, Fg 17.57, 1100
- Helicoidea, Fg 17.72, 1113
- Hemidonacidae, Fg 8.17, 331
- Heterobranchia, Fg 15.179, Fg 15.180, Fgs 15.182–15.187
- Heterodonta, 301
- Hiattellidae, Fg 8.44, 301, 370, 371
- Hiattelloidea, Fg 8.44, 370
- Hipponicidae, Fg 15.123, 770
- Hydatinidae, Fg 16.23, 922, 945
- Hydrobiidae, Fg 15.111, 752
- Hydrocenidae, Fg 15.76, 701
- Hydrococcidae, Fg 15.118, 763
- Hyriidae, Fg 1.67, Fg 7.1, Fg 7.9, 289, 297
- Idiosepiidae, 514
- Incirrata, 453
- internalisation, Fg 14.7, 573
- Iravadiidae, Fg 15.110, 752
- Ischnochitonidae, Fg 3.34
- Isognomonidae, Fg 6.10, 264
- Janthinidae, Fg 15.151, 814
- Janthinoidea, Fg 15.151, Fg 15.152
- Jouannetinae, Fg 8.49
- Juliidae, 964, 965
- Kelliellidae, 350
- Laevicardiinae, 331
- Laevidentaliidae, Fg 10.16
- Lamellaridae, Fg 15.133
- Lamellariinae, 789
- Lametilidae, 239
- Laternulidae, Fg 4.2, Fg 9.10, 410, 411
- Laubierinae, Fg 15.139, 798
- Lepetellidae, Fg 15.45, 659
- Lepetelloidea, Fg 15.45
- Lepetidae, Fg 15.38
- Lepidopleuridae, Fg 3.31
- Limacidae, 1102
- Limacinidae, Fg 16.61, 981
- Limacoidea, Fg 17.65, Fgs 17.61–17.63, 1101
- Limidae, Fg 6.13, 267
- Limoidea, Fg 6.13
- Limopsidae, Fg 6.5, 258
- Limopsoidea, Fgs 6.5–6.7, 253, 258
- Liotiinae, Fg 15.55, 673
- Litiopidae, Fg 15.87, 707, 714
- Littorinidae, Fg 15.100, 738
- Littorinoidea, Fg 15.100, Fg 15.101
- Loliginidae, 517
- loss in Eulimidae, 614
- loss in prosobranchs, 614
- Lottiidae, Fg 15.39, Fg 15.40
- Lottinae, Fg 15.39
- Lucinidae, 310
- Lucinoidea, Fgs 8.4–8.7, 309
- Lymnaeidae, Fg 17.31, 1069
- Lymnaeoidea, Fg 17.35, Fgs 17.31–17.33, 1069
- Lyriinae, Fg 15.164
- Mactridae, Fg 8.22, 337, 338
- Mactroidea, Fgs 8.22–8.24, 336
- Mactromyidae, Fg 8.7, 315
- Malleidae, Fg 4.2, Fg 6.9, 262
- Mallettiidae, Fg 5.4, 239
- Margaritinae, Fg 15.62, 682
- Marginellidae, Fg 15.167, 838
- Marginellinae, Fg 15.167
- Martesiinae, Fg 8.48
- Mathildidae, Fg 15.182, 859
- Megaspiridae, Fg 17.48, 1088
- Melongenidae, 831
- Mesodematidae, 339
- Mesodesmatidae, Fg 8.23, 339
- microstructure, Fg 1.12, 12
- Mitridae, Fg 15.169, 841
- Mitrinae, Fg 15.169
- Modulidae, Fg 15.96, 707, 730
- Mopaliidae, Fg 3.37
- Moruminidae, Fg 15.166, 837
- Muricidae, Fg 14.4, Fg 15.156, 820, 822
- Muricoidea, 820
- Myidae, Fg 8.41, 366
- Myochamidae, Fg 9.14, 418
- Myoida, 362
- Myoidea, Fg 8.41, Fg 8.42, 363
- Mytilidae, Fg 6.1, 197, 251
- Mytiloida, Fg 6.1, 250
- Nacellidae, Fg 14.4, Fg 15.36, 647
- Nassariidae, Fg 15.161, 829
- Nassariinae, Fg 15.161
- Naticidae, Fg 15.134, 790
- Naticinae, 790
- Naticoidea, Fg 15.134
- Nautilidae, Fg 12.12, Fg 12.13, 494
- Nautiloida morphology, Fg 12.3
- Nautiloidea, 485
- Nautilus*, 453
- Nautilus pompilius*, Fg 12.12
- Neilonellidae, Fg 5.5, 239

INDEX

shell *continued*

- Neogastropoda, Fg 15.156, Fgs 15.158–15.171
- Neoleptonidae, Fg 8.10, 320
- Neritidae, Fg 15.72, 695
- Neritoidea, 694
- Neritopsidae, Fg 15.71, 694
- Neritopsina, Fg 15.71, Fg 15.72, Fg 15.74, Fg 15.76, Fg 15.77, 694
- Neritopsis radula, Fg 15.71
- Noetiidae, Fg 6.4, 257
- Notaspidea, 977
- Notodiaphanidae, Fg 16.39, 959
- Nucinellidae, 244
- Nuculanidae, Fg 4.2, Fg 5.6, 239
- Nuculanoidea, 239
- Nuculidae, Fg 5.2, Fg 5.3, 237
- Octopodidae, 549
- Olivellinae, 835
- Olividae, Fg 15.165, 835
- Olivinae, Fg 15.165, 835
- Omalogyridae, Fg 15.185, 864
- Omalogyroidea, Fg 15.185, 864
- Omniglyptidae, Fg 10.18
- ontogeny in Tellinoidea, 342
- Opisthobranchia, Fg 16.63, 922
- Opisthoteuthidae, 545
- Orbitostellidae, Fg 15.180, 856, 857
- orientation and locomotion, 614
- Orthurethra, 1080
- Osteopeltidae, 663
- Ostreidae, Fg 6.15, 270
- Ostreinae, 270
- Ostreoidae, Fg 6.14, Fg 6.15
- Ostreoida, 268
- Otinoidea, 1062
- Ovulidae, Fg 15.131, 784
- Ovulinae, 784
- Oxynoidae, 963
- Palaeoheterodonta, Fg 7.1, 289
- Pandoridae, Fg 9.13, 415
- Pandoroidea, 415
- Parilimyidae, Fg 9.7, 406
- Partuloidea, Fg 17.45, 1085
- Patellidae, Fg 15.35
- Patellogastropoda, 643
- Patelloidinae, Fg 15.40
- Pectinidae, Fg 6.18, 275
- Pectinina, 275
- Pectinodontinae, Fg 15.37, 648
- Pectinoidea, Fg 6.18, Fg 6.19, 275
- Pendromidae, 692
- Peraclididae, Fg 16.63, 983
- Periplomatidae, Fg 9.9, 409, 410
- Permophoridae, 322
- Personidae, Fg 15.140, 798
- Petricolidae, Fg 8.39, 361
- Phaliinae, 795
- Pharidae, Fg 8.26, 341
- Phasianellinae, 678
- Phenacolepadidae, Fg 15.74, 700
- Philine angasi*, Fg 16.4
- Philinidae, Fg 16.29, 950
- Philobryidae, Fg 6.7, 260
- Pholadidae, Fg 8.45, Fgs 8.47–8.50, 362
- Pholadinae, Fg 8.47, 375
- Pholadoidea, Fg 8.45, Fg 8.52, Fgs 8.47–8.50, 372
- Pholadomyoidea, 405
- Photinae, Fg 15.159
- Physidae, Fg 17.35, 1074
- Pickworthiidae, Fg 15.101, 739
- Pinnidae, Fg 4.2, Fg 6.12, 265
- Pinnoidae, Fg 6.12
- Pisanianuridae, Fg 15.141, 799
- Pisaniinae, Fg 15.159
- Pitarinae, 360
- Placunidae, Fg 6.21, 281
- Planaxidae, Fg 15.91, 707, 722
- Planorbidae, Fg 17.33, 1072
- Plesiotrochidae, 736
- Pleurodiscidae, 1084
- Pleurotomariidae, Fg 15.51, 664, 666
- Pleurotomarioidea, 664
- Plicatulidae, Fg 1.16, 273
- Polygyroidea, Fg 17.68, 1110
- Pomatiopsidae, Fg 15.112, 755
- Poromyidae, Fg 9.17, 422
- Potamididae, Fg 15.92, 707, 724
- Propeamussiidae, 278
- Propilidinae, Fg 15.38
- Protobranchia, Fg 5.2
- Protocardiinae, 331
- Psammobiidae, Fg 8.30, 345
- Pseudococculinidae, Fg 15.45, 663
- Pseudolivinae, Fg 15.165
- Ptenoglossa, Fg 15.148, Fg 15.150
- Pteriidae, Fg 4.2, Fg 6.8, 261, 262
- Pterioidea, 261
- Pterioidea, Fgs 6.8–6.11, 261
- Pteriomorpha, 249
- Ptychactractinae, Fg 15.158, 825
- Pulmonata, 1037, 1039
- Pulsellidae, Fg 10.20
- Pulvinitidae, Fg 6.11, 265
- Punctidae, Fg 17.54
- Pupillidae, Fg 14.4, Fg 17.42, 1082
- Pupilloidea, Fg 17.42, Fg 17.44, 1082
- Pupinidae, Fg 15.79, 704, 705
- Pyramidellidae, Fg 15.186, 865, 867
- Pyramidelloidea, Fg 15.186, Fg 15.187, 865
- Pyreninae, Fg 15.160
- Ranellidae, Fg 15.142, 799
- Rastodontidae, Fg 15.104, 744
- reduction and carnivory, 1039
- Retusidae, Fg 16.28, 949
- Rhytididae, Fg 17.51, 1091
- Rhytidoidea, Fg 17.51, 1091
- Ringiculidae, Fg 16.24, 946
- Ringiculoidea, 946
- Rissoellidae, Fg 15.184, 862
- Rissoelloidea, Fg 15.184, 862
- Rissoidea, Fg 15.108, 749
- Rissooidea, Fgs 15.105–15.120, 745
- role of calcium, 13
- Rostroconchia, 223
- Runcinidae, 958
- Sacoglossa, 961, 962
- Sareptidae, Fg 5.7, 240
- Scaliolidae, Fg 15.97, 707, 732
- Scaphellinae, Fg 15.164
- Scaphopoda, Fgs 10.13–10.20, 432
- Schizochitonidae, Fg 3.36
- Scissurellidae, Fg 15.52, 664, 666
- Seguenziidae, Fg 15.70, 692
- Seguenzioidea, 692
- Semelidae, Fg 8.29, 344
- Sepiidae, Fg 13.3, 505
- Sepioidea, Fg 13.3, 453, 455, 504
- Sigmurethra, 1086
- Siliculidae, 239
- Siliquariidae, Fg 14.4, Fg 15.89, 707, 718
- Sininae, 790
- Siphonariidae, 1039, 1068
- Siphonarioidea, 1067
- Skeneidae, Fg 15.69, 691
- Smaragdinellidae, Fg 16.35, 955
- Solariellinae, Fg 15.66, 687
- Solecurtidae, 346
- Solemyidae, Fg 5.2, Fg 5.8, 241
- Solenidae, Fg 4.2, Fg 8.25, 341
- Solenoidae, Fg 8.25, Fg 8.26, 301, 306, 340
- Sphaeriidae, Fg 8.36, 355
- Spirulidae, Fg 13.1, 504
- Spondylidae, Fg 6.19, 278
- Sportellidae, Fg 8.11, 321
- Stenothyridae, Fg 15.120, 765
- Stomatellinae, Fg 15.64, 685
- Streptaxidae, Fg 17.50, 1090
- Streptaxoidea, Fg 17.50, 1090
- Strombidae, Fg 15.121, 766
- Stromboidea, Fg 15.121, Fg 15.122, 766
- Struthiolariidae, Fg 15.122, 768
- Stylommatophora, 1079
- Subulinidae, Fg 17.47, 1087
- Succineidae, Fg 17.66, 1108
- Succinoidea, Fg 17.66
- Sunettinae, 358
- Systellommatophora, 1060
- Tapetinae, 360
- Tellinidae, Fg 8.28, 343
- Tellinoidea, Fg 8.28–8.30, Fg 8.32, 306, 342
- terebrid protection, 851
- Terebridae, 846, 850
- Teredinidae, Fg 8.51, Fg 8.52, 376
- Teredininae, Fg 8.52
- Testacellidae, Fg 17.65, 1107
- Teuthoidea, 453, 515
- Thecosomata, 981
- Thiariidae, Fg 15.94, 707, 727
- Thraciidae, Fg 9.8, 408
- Thracioidea, 407
- Thyasiridae, Fg 8.5, 314
- Tonnidae, Fg 15.144, 802
- Tonnoidea, Fg 15.144, Fgs 15.136–15.142, 792, 793
- Trapeziidae, Fg 8.33, 301, 348
- Tricoliinae, Fg 15.59, 677
- Tridacnidae, Fg 4.2, Fgs 8.18–8.20, 333
- Tridacnoidea, Fg 8.18, Fg 8.20, 301, 332
- Trigoniidae, Fg 7.1, Fg 7.8, 290, 295
- Trigonioida, Fg 7.1
- Trigonoidea, 295
- Trigonostominae, 845
- Trimusculidae, Fg 17.38, 1039
- Trimusculoidea, Fg 17.38
- Triphoridae, Fg 15.148, 809
- Triphoroidea, Fg 15.148, Fg 15.150, 808
- Triviidae, Fg 15.132, 786, 787
- Triviinae, 787
- Trochidae, Fgs 15.61–15.68, 680
- Trochinae, 683
- Trochoidea, 671, 672
- Trochomorphidae, Fg 17.62, 1104
- Truncatellidae, Fg 15.114, 758
- Tudiclinae, 825
- Turbinellidae, Fg 15.158, 824
- Turbinellinae, 825
- Turbinidae, Fgs 15.55–15.60, 673
- Turbininae, Fg 15.57, 675
- Turridae, Fg 15.174, 846, 848
- Turritellidae, Fg 14.4, Fg 15.88, 569, 707, 716
- Tylodinae, 977
- Umbroniinae, Fg 15.68, 689
- Umbraculidae, 978
- Ungulinidae, Fg 4.2, Fg 8.6, 315
- Unionoida, Fg 7.1, 296
- Valloniidae, Fg 17.44, 1084
- Valvatoidea, Fg 15.179, Fg 15.180, 855
- Vampyroreuthidae, 542
- Vanikoridae, Fg 15.124, 771
- Vanikoroidea, Fgs 15.123–15.125, 769
- Vasinae, Fg 15.158, 825
- Velutinae, 786, 789
- Velutinoidea, Fg 15.132, Fg 15.133
- Veneridae, Fg 4.1, Fg 4.2, Fg 8.37, Fg 8.38, 301, 356
- Veneroida, 306
- Veneroidea, Fgs 8.37–8.40, 301, 306, 355
- Vermetidae, 778, 779
- Vermetoidea, 778
- Verticordiidae, Fg 9.16, 420
- Vesicomysidae, 350
- Vetigastropoda, Fgs 15.51–15.70, 674
- Vitrinellidae, Fg 15.119, 763, 765
- Viviparidae, Fg 15.81, 706
- Volutidae, Fg 15.164, 833
- Volutomitridae, Fg 15.170, 842
- Zolvatellidae, 962
- Volviniae, 784
- Volvtellidae, 962
- Xenophoridae, Fg 14.4, Fg 15.128, 776
- Xenophoroidea, Fg 15.128
- Xylodisculidae, 858
- Xylophaginae, Fg 8.50
- Zonitidae, Fg 17.61, 1104
- shell, embryonic
- Planaxidae, Fg 14.36
- shell rotation, Tridacnoidea, 306
- shell, secondary, Argonautidae, 453
- shell apex, Scaphopoda, 431
- shell asymmetry, Bivalvia, 198
- shell boring, Gastrochaenidae, 369
- shell cementation
- Chamidae, 307
- Cleidotheriidae, 307, 419
- Dimyidae, 307
- Gryphaeidae, 307
- Myochamidae, 307
- Ostreidae, 307
- Pectinidae, 307
- Plicatulidae, 307
- Spondylidae, 307
- shell chamber
- Gastrochaena tasmanica*, 369
- Gastrochaenidae, 369
- shell characters, Hydridae, Fg 7.9
- shell cleaning, 613
- shell collecting
- Cassis cornuta*, 115
- Charonia tritonis*, 115
- economic importance, 76
- taxa at risk, 76
- shell composition
- Polyplacophora, 163
- shell exports, Fg 1.85
- shell formation
- pulmonate embryo, 1051
- shell geometry
- adaptive features, 12, 570
- shell gland
- Bivalvia, 216
- pulmonate embryo, 1051
- shell modification, 572
- Caecidae, Fg 14.6
- Conidae, Fg 14.6
- Ellobiidae, Fg 14.6
- Gastropoda, Fg 14.6
- Muricidae, 572
- Truncatellidae, Fg 14.6
- shell morphology
- Bivalvia, Fg 4.4
- Gastropoda, 569
- Mollusca, 12
- Polyplacophora, 163
- taxonomic implications, 570
- Veneridae, Fg 4.4
- shell muscles
- Addisoniidae, Fg 15.50
- Bathypheophyllidae, Fg 15.50
- Bathysciadiidae, Fg 15.43
- Choristellidae, Fg 15.50
- Cocculinidae, Fg 15.42
- Cocculinoidea, 655
- Lepetellidae, Fg 15.50
- Lepetelloidea, Fg 15.50, 656
- Mollusca, 3, 13
- ontogeny, 613
- Osteopeltidae, Fg 15.50

- prosobranchs, 613
 - Pseudococculinidae, Fg 15.50
 - Pyropeltidae, Fg 15.50
 - Scissurellidae, 666
- shell organs, Polyplacophora, 171
- shell ornamentation, 614
 - Chamidae, 308
 - as protection, 614
- shell polymorphism
 - sexual expression, 215
- shell reduction, 1039
 - Opisthobranchia, 915
- shell regeneration, Pinnidae, 266
- shell resorption, 572
 - Ellobiidae, 572
 - Neritidae, 572
 - Olivella, 572
 - Turritellidae, 572
- shell sculpture
 - adaptive features, 571
 - Bivalvia, Fg 4.3, 199
- shell secretion
 - echinospira larva, 787
- shell shape
 - coiling parameters, Fg 14.5
 - Crassostreinae, 272
 - evolutionary factors, 614
 - Gastropoda, Fg 14.4, 570
 - habitat, Bivalvia, 199
 - Heterodonta, 301
 - life style, 614
 - locomotion, 575
 - Lophinae, 271
 - Ostreina, 268
 - Spondylidae, 278
 - Unionidae, 199
- shell slit
 - Pleurotomarioidea, 664
 - Scissurellidae, 666
- shell thickness
 - and latitude, 412
- shell ultrastructure, 261, 280, 424, 614
 - Acmaeidea, 640
 - Anomalodesmata, 202, 398
 - Anomiidae, 280
 - Arcoidea, 253
 - Bivalvia, Fg 4.7, 198, 202
 - Cambrian, 223
 - Carditidae, 322
 - Carditoidea, 322
 - Chamidae, 308
 - Chamoidea, 302
 - Cleidotheridae, 419
 - complex crossed-lamellar, Fg 4.7
 - Corbiculidae, Fg 4.7, 354
 - Corbulidae, 366
 - Crassatellidae, 326
 - Crassatelloidea, 325
 - Cuspidariidae, 424
 - Cyamiidae, 319
 - Fissurelloidea, 669
 - foliated calcite layer, Fg 4.7
 - Glossidae, 352
 - Heterodonta, 202, 301, 302
 - Lepetopsina, 640
 - Limidae, 267
 - Limoida, 250, 267
 - Lottiidae, 640
 - Lyonsiidae, Fg 4.7, 398
 - Mactroidea, 336
 - Myoidea, 363
 - Mytiloida, 250
 - Nacelloidea, 640
 - nacre, Fg 4.7
 - Neritidae, 696
 - Ostreidae, Fg 4.7
 - Ostreina, 268
 - Ostreoida, 250, 268
 - Palaeoheterodonta, 202
 - Palaeotaxodonta, 202
 - Patellidae, 640
 - Patellogastropoda, Fg 15.32, 640
 - Patelloidea, 640
 - Pectinidae, 275
 - Pectinodontinae, 648
 - Pectinoidea, 275
 - Periplomatidae, 410
 - Pinnidae, 265
 - Placunidae, 282
 - Pleurotomarioidea, 664
 - Poromyidae, 422
 - prismatic layer, Fg 4.7
 - Propeamussiidae, 278
 - Protobranchia, 202
 - Pterioidea, 250
 - Pterioidea, 261
 - Pteriomorphia, 202, 250
 - Pulmonata, 1039
 - Scaphopoda, 432
 - Spondylidae, 278
 - Tellinoidea, 342
 - Thraciidae, 408
 - Trapeziidae, 348
 - Tridacnoidea, 332
 - Trigoniidae, 295
 - Veneridae, 356
 - Veneroidea, 302
 - Verticordiidae, 420
- shell variation
 - Hyriidae, 297
 - Neritina violacea, 696
- shell weight, Tridacnidae, 333
- shell/body relationship
 - Bivalvia, Fg 4.10, Fg 4.11
 - Lucinidae, Fg 4.10
 - Mytilidae, Fg 4.11
 - Nuculidae, Fg 4.10
 - Pharidae, Fg 4.10
 - Pholadidae, Fg 4.10
 - Pinnidae, Fg 4.11
 - Tellinidae, Fg 4.10
 - Yoldiidae, Fg 4.10
- Sherbornia, 741
- Sherbornia mirabilis, 739, 741
- shell, Fg 15.101
- Sherborniidae, 740, 808
- shipworms, Pl 16, 371
 - economic significance, 76, 221
- shoaling behaviour
 - Teuthoidea, 473
- Siboga, 145, 156, 432
- side-gilled slug, Pl 33
- Sigapatella, 774
- Sigapatella calyptraeformis
 - shell, Fg 15.126
- Sigara, 355
- Sigaretornus, 765
- Sigaretornus planus
 - commensal, 764
 - egg capsules, 764
 - shell, Fg 15.119
- Sigatica, 791
- sight, cephalopod predation, 51
- Sigmurethra, 1046, 1047
 - affinities, 1080
 - classification, 1086
 - description, 1086
 - form of ureter, 581
- Signepupina, Fg 15.79
- Siliculidae, characters, 239
- Siliqua, 341
 - fourth pallial aperture, 398
 - on sandy beaches, 37
- Siliquaria, 718, 720
- Siliquaria australis, shell, Fg 15.89
- Siliquaria weldii, 720
- Siliquariidae, Fg 14.4, Fg 15.89
 - affinities, 718, 720
 - characters, 718
 - family treatment, 718
 - sperm transfer, 632
- Silurian, 95
 - Actinocerida, 490
 - Carditoidea, 322
 - Crassatelloidea, 325
 - Lucinidae, 310
 - marine transgressions, 90
 - Nautiloidea, 485, 489
 - Solemyidae, 235
- Siluriphorus
 - Devonian, 95
- Silver Gull
 - as chiton predator, 184
 - host of Austrotilharzia terrigalensis, 69
- Simnia, 784, 786
 - as fossils, 786
 - use of proboscis, 622
- Simnia patula
 - egg mass, 785
 - veliger, 786
- Simroth gland, Rathousiidae, 1049
- Simulathena, 722
- simultaneous hermaphroditism, 633
- Sinezona, 666
 - shell, Fg 15.52
- Singleton, Frederick, 11
- sinistral whorls
 - Triphoridae, 809
- Sinistrobranchia, 854
- Sinonovacula, 341, 346
 - siphons, 341
 - teeth, 341
- Sinonovacula constricta
 - mariculture, 341
- Sinployea intensa, 87
- Sinuitina
 - Carboniferous, 95
 - Silurian, 95
- Sinum, 790, 791
 - shell, 790
- Sinum zonale
 - external appearance, Fg 15.134
 - shell, Fg 15.134
- Sinumelon, 56, 81
 - distribution, Fg 1.93
 - range size, 87
 - shell, 1112
- Sinumelon amatensis
 - distribution, Fg 1.93
- Sinumelon bednalli
 - distribution, Fg 1.93
- Sinumelon bitaeniatum
 - shell, Fg 17.69, 1112
- Sinumelon dulcensis
 - distribution, Fg 1.93
- Sinumelon expositum
 - distribution, Fg 1.93
- Sinumelon gillensis
 - distribution, Fg 1.93
- Sinumelon hullanum
 - distribution, Fg 1.93
- Sinumelon musgravesi
 - distribution, Fg 1.93
- Sinumelon pedasum
 - distribution, Fg 1.93
- Sinumelon perinflatum
 - distribution, Fg 1.93
- Sinumelon pumilio
 - distribution, Fg 1.93
- Sinumelon remissum
 - water loss, Tb 17.1
- Sinumeloninae, 1112
- sinuses, 581
 - cephalopedal, 581
 - Polyplacophora, 168
 - subrenal, 581
 - visceral, 581
- Sinutor, 686
 - in Australia, 686
- Sinutor incertum
 - shell, Fg 15.65
- Siphocypraea, as fossils, 784
- siphon
 - Conidae, 852
 - Marginellidae, Fg 15.168
 - Nassariidae, Fg 15.161
 - Nassariinae, Fg 15.161
 - Neogastropoda, Fg 15.161, Fg 15.165, Fg 15.168
 - Olividae, Fg 15.165
- siphons, 364
 - Anomalodesmata, 399
 - Arcticoidea, 348
 - Bivalvia, Fg 4.1, Fg 4.8, 195
 - Bivalvia, 206
 - Cardidae, Fg 8.16, 329
 - Clavagellidae, Fg 9.12, 414
 - Cleidotheridae, 419
 - Corbiculoidea, 352
 - Corbulidae, Fg 8.42
 - Cuspidariidae, Fg 9.5, 400, 424
 - Cuspidarioidea, 399
 - Cyamiidae, Fg 8.9
 - Cyamioida, 318
 - Donacidae, Fg 4.9, Fg 8.32, 347
 - Fimbriidae, Fg 8.4, 313, 314
 - Galeommatoidea, 316
 - Gastrochaenidae, Fg 8.43, 367, 368
 - Glauconomidae, Fg 8.40, 362
 - Glossidae, 352
 - heterodont radiation, 302
 - Heterodonta, 301–303
 - Hiatellidae, 370, 371
 - Hiatelloidea, 370
 - Laternulidae, Fg 9.3, Fg 9.10, 411, 412
 - Lithophaginae, 251
 - Lucinidae, 311
 - Mactridae, Fg 8.21, 337, 338
 - Mactroidea, 302, 336
 - Malletiidae, Fg 5.4, 239
 - Martesiinae, 375
 - Mesodesmatidae, Fg 8.23
 - Myidae, Fg 8.41
 - Myochamidae, Fg 9.14, 418
 - Myoida, 362
 - Myoidea, 302, 363
 - Mytiloida, 250
 - Neilonellidae, 239
 - Neoleptonidae, Fg 8.10, 321
 - Nuculanidae, Fg 5.6, 239
 - Pandoridae, 416
 - Pandoroidea, 415
 - Parilimyidae, Fg 9.5, Fg 9.7, 400, 406
 - Periplomatidae, Fg 9.9, 409, 410
 - Petricolidae, Fg 8.39
 - Pharidae, Fg 4.9
 - Pholadidae, Fg 8.45
 - Pholadomyoidea, 406
 - Poromyidae, Fg 9.3, Fg 9.5, Fg 9.17, 400, 422
 - Poromyoidea, 399
 - predation, Anomalodesmata, 400
 - and predators, 304
 - Pteriomorphia, 249
 - Sareptidae, Fg 5.7
 - Semelidae, Fg 8.29
 - Solecurtidae, 346
 - Solenidae, Fg 4.22
 - suctorial, 399
 - tentacles, 399
 - Thraciidae, 408
 - Thracioidea, 407
 - Veneridae, Fg 4.1, Fg 4.9
 - Verticordiidae, Fg 9.5, Fg 9.16, 400, 420
 - Verticordioida, 399
- siphons, evolution
 - Cardioidea, 307
 - Mactroidea, 307
 - Tellinoidea, 307
 - Veneroidea, 307

INDEX

- siphonal hood
hydraulic eversion, 401
- siphonal length
and habitat, 304
- siphonal process
hydraulic extension, 364
- Myoidea, 364
- siphonal retractor muscles
Anomalodesmata, 399
- Bivalvia, 206
- Cuspidariidae, 424
- Gastrochaenidae, 368
- Glauconomidae, Fg 8.40
- Lithophaginae, 251
- Mactridae, Fg 8.21
- Mesodesmatidae, 339
- Parilimyidae, 399
- Pharidae, Fg 8.26
- Pholadomyidae, 399
- Tellinidae, Fg 8.27
- Thraciidae, 408
- Verticordiidae, 399
- siphonal sense organs
Anomalodesmata, 401
- septibranchs, 401
- siphonal tentacles, 424
- Poromyidae, Fg 4.18, 422, 423
- Verticordiidae, 420
- siphonal types, Bivalvia, Fg 4.8
- Siphonaria*, 188, 1045
- diversity in Australia, 1068
- egg masses, 25
- osmoregulation, 1045
- stomach, 1068
- taxonomy, 1068
- veliger, 27
- Siphonaria alternata*
mantle cavity, Fg 14.19
- Siphonaria atra*
shell, Fg 17.30
- Siphonaria baconi*, 1068
- Siphonaria denticulata*, 1068, 1069
- egg ribbons, Fg 17.30, 1068
- interspecific competition, 31
- radula, Fg 17.30
- Siphonaria diemenensis*, Pl 31, 1068, 1069
- Siphonaria funiculata*, 1068, 1069
- Siphonaria japonica*
homing behaviour, 577
- Siphonaria jeanae*
reproductive tract, Fg 17.30
- spermatophore, Fg 17.30
- Siphonaria laciniosa*, shell, Fg 17.30
- Siphonaria tasmanica*, 1069
- Siphonaria virgulata*, 1068
- interspecific competition, 31
- Siphonariidae, Fg 14.19, Fg 17.30, Pl 31
- family treatment, 1068
- kidney, 1045
- on rocky shores, 29
- Siphonarioidea, description, 1067
- siphon-nipping,
Heterodonta, 304
- Veneridae, 358
- Siphonodentaliinae, 446
- Siphonodentalium*, 431, 446
- Siphonodentalium eboracense*, 446
- Siphonodentalium galathea*, 446
- habitat, 437
- siphonophore tentacles
use by octopods, 474
- siphonophores
associations, Janthinidae, 814
- as janthinid prey, 813
- and *Pterotrachea coronata*, 807
- siphonoplax
Jouannetiinae, 376
- Pholadidae, Fg 8.45, Fg 8.49
- Siphonopoda, 3
- Siphopatella*, 774
- Siphopatella walshi*
distribution, 774
- Siphopteron*, 954
- siphuncle,
Actinocerida, Fg 12.6
- Cephalopoda, 454
- Discosorida, Fg 12.7
- Endocerida, Fg 12.5
- Nautilidae, Fg 12.11
- Nautiloidea, 485
- Oncocerida, Fg 12.4
- siphuncular deposits
Nautiloidea, 486
- siphuncular tube
Nautiloidea, 485
- Sipuncula
as mitrid prey, 842
- as muricid prey, 823
- as prey of Tudiclinae, 825
- relationship to molluscs, 1
- spiral cleavage, 22
- as turrid prey, 850
- Sirius*, 6, 775
- Sirius badius*
shell, Fg 15.127
- size
Architeuthidae, 527
- Carinariidae, 806
- Cephalopoda, 453
- Cerithiopsidae, 811
- Cypraeidae, 782
- Epitoniidae, 814
- Idiosepiidae, 514
- Muricidae, 822
- Volutidae, 833
- skeletal cartilages
Cephalopoda, 453
- Skenea*, 691
- radula, 691
- Skeneidae, Fg 15.69, Tb 15.1
- in Australia, 672
- family treatment, 690
- Liotiine taxa, 673
- polyphyly, 691
- Skeneinae, 673
- Skenella*
distribution, 743
- Skenella westralis*
radula, Fg 15.102
- shell, Fg 15.102
- skin
Cephalopoda, 453
- skin structures
Cephalopoda, 454
- slipper limpets, 44
- slit-limpet, Fg 1.23
- slow muscle, Bivalvia, 204
- slugs, Pulmonata, 1039
- Smaragdia trigena*, 695
- Smaragdiinae
in Australia, 695
- Smaragdinella*, 954–956
- Smaragdinella calyculata*, Fg 16.35
- external appearance, Fg 16.35
- Smaragdinella viridis*, Fg 16.35
- shell, Fg 16.35
- Smaragdinellidae*, Fg 16.16, Fg 16.35
- diet, 937
- family treatment, 955
- Smeagol*, 1062, 1063
- affinities, 1062
- distribution, 1062
- diversity, 1062
- external appearance, 1062
- habitat, 1052
- restricted range, 115
- Smeagol hiliaris*
alimentary tract, Fg 17.25
- external appearance, Fg 17.25
- Smeagol manningi*
nervous system, 1063
- Smeagol parvulus*, radula, Fg 17.25
- Smeagol phillipensis*
reproductive tract, Fg 17.25
- Smeagolidae, Fg 17.25
- affinities, 1062
- family treatment, 1062
- Smith, E.A., 196, 337, 352, 354
- snout, 766
- gastropods, 619
- Hipponicidae, 770
- Strombidae, 766
- São Tomé Island, 1102
- Sohgenia*, 969, 970
- Solander, Carl, 6
- Solanderian Province, 78, 593
- Cerithiopsidae, 811
- Solanderian Region
characteristic molluscs, 1057
- non-marine molluscs, 81
- Solariella nuda*
radula, Fg 15.66
- Solariella peramabilis*
head-foot, Fg 15.66
- Solariellinae, 679, 682
- in Australia, 687
- description, 687
- Solatissonax*, 861, 862
- Solatissonax injussa*
endemic, 861
- Solecurtidae, Fg 8.31, 343
- family treatment, 346
- Solecurtus*, 346
- Tertiary, 101
- Solecurtus sulcatus*, 346
- external appearance, Fg 8.31
- Solem, Alan, 1039
- Solemya*, Pl 10, 241, 243
- Cainozoic, 314
- deposit-feeding, 243
- research value, 244
- swimming, 206, 241
- Solemya atacama*, distribution, 243
- Solemya australis*, 241
- distribution, 243
- habitat, 243, 244
- shell, Fg 5.8
- swimming, 242
- type locality, 236
- Solemya borealis*, 243
- Solemya cf. australis*
pallial morphology, Fg 5.8
- '*Solemya*' *holmwoodensis*
as fossils, 244
- Solemya parkinsonii*, 241
- distribution, 243
- Solemya reidi*, 242, 243
- burrow habitat, Fg 5.10
- distribution, 243
- pericalymma larva, Fg 5.8
- population density, 243
- reproduction, 243
- shell, Fg 5.8
- sulphide oxidase, 243
- sulphide oxidation, 315
- swimming cycle, Fg 5.9
- valve dentition, Fg 5.2
- ventilatory behaviour, 242
- Solemya (Solemyarina)*
as fossils, 244
- Solemya solen*, distribution, 243
- Solemya terraereginae*, 241
- habitat, 244
- as spiny lobster prey, 244
- Solemya togata*, distribution, 243
- Solemya valvulus*, distribution, 243
- Solemya velesiana*, 241
- ctenidial lamella, Fg 5.11
- ctenidial mitochondria, 243
- distribution, 243
- habitat, 243
- internal morphology, Fg 5.11
- swimming, 242
- Solemya velum*, 242, 243
- Solemyarina*, 241
- Solemyidae, Fg 5.2, Fgs 5.8–5.11, Pl 10, 225
- family treatment, 241
- genera, 241
- larval metamorphosis, 243
- sulphide oxidase, 243
- symbiotic bacteria, 207
- ventilatory behaviour, 242
- Solemyoidea, 225, 235
- characters, 225
- decription, 241
- shared features, Nuculoida, 235
- sulphide-oxidising bacteria, 235
- Solen*, 341
- Aboriginal resources, 341
- autotomy, siphons, 219
- diversity, 341
- siphon, Fg 4.22
- swimming, 206
- Solen aff. exiguus*
pallial tentacles, 341
- Solen aureomaculatus*
distribution, 341
- Solen correctus*, distribution, 341
- Solen fonesii*, distribution, 341
- Solen grandis*, 341
- shell, Fg 8.25
- Solen kajiyamai*, distribution, 341
- Solen sloani*, distribution, 341
- Solen vaginoides*, Pl 13
- distribution, 341
- shell form, Fg 4.2, 199
- Solena*, 341
- Solenidae, Fg 4.2, Fg 4.22, Fg 8.25, Pl 13, 341
- family treatment, 341
- Solenosconcha
see Scaphopoda, 5
- Solenogastres, 2, 149
- Solenosconcha, 340
- amino acids, 340
- description, 340
- mantle apertures, 204
- Solenomorpha*, Tb 1.6
- Soleolifera, 1047, 1064
- Soletellina*, 345
- habitat, 345
- shell, 345
- Soletellina alba*, 343, 346
- Soletellina biradiata*, 346
- Soletellina donacioides*
distribution, 346
- Soletellina siliquens*, 343, 346
- Solutiscala*, radula, 814
- somersaulting, *Notarchus*, 976
- Sonderopelta coriacea*, 180
- Sonninia*
Jurassic, 97
- Sorbeosconcha, Tb 15.1, 707
- affinities, 703
- characters, 703
- component groups, 610
- relationships, 610
- taxa, 703
- sorting area, Bivalvia, Fg 4.13
- South African gastropods
in Australia, 593
- South Georgia
Struthiolariidae, 768

- South-East Australian Province, 101
 southern crypt dweller, 370
 southern gaper, 370
 southern scallop, Pl 13
 fishery, 73
 Sowerby, George Brettingham, 8, 162, 196, 594
 Sowerby, James, 8
 Sowerby family, 1038
 'space cells,' 611
 spadix
 Nautilidae, Fg 12.11
 Nautiloidea, 454
 Nautilus, 469, 494
Sphaerospira bloomfieldi
 sperm ultrastructure, Fg 17.19
 Spanish Dancer, Fg 16.9
Spathoteredo
 pallets, 378
Spathoteredo obtusa
 pallet, Fg 8.54
 spawn, Caenogastropoda, 635
 spawn ribbon
 Trochidae, Fg 15.21
 Vetigastropoda, Fg 15.21
 spawning, 436, 439
 Anomalodesmata, 401
 Anomiidae, 281
 Bivalvia, 25, 216
 broadcast, 24
 Cephalopoda, 469
 Cleidothaeridae, 420
 Crassostreinae, 272
 Ctenopterygidae, 531
 Dentaliida, 436
 Donacidae, 347
 Heterodonta, 303
 Histiot euthidae, 529
 Loliginidae, 519
 Mesodesmatidae, 339
 Myoida, 216
 Myoidea, 363
 Mytilidae, 251
 Onychoteuthidae, 524
 Ostreinae, 270
 Patellogastropoda, 25
 Polyplacophora, 25, 173
 Pteriormorphia, 216
 Scaphopoda, 25
 synchronous, 24
 Tellinidae, 343
 Tridacnidae, Pl 14, 335
 Trochidae, Fg 15.22
 Trochoidea, 672
 Veneridae, 356
 Veneroida, 216
 Vetigastropoda, Fg 15.22, 25
 spawning, multiple, Coleoidea, 471
 spawning cues
 Corbiculoidea, 303
 Myoida, 303
 Pteriormorphia, 249
 Tellinidae, 303
 Veneridae, 303
 spawning hormone, Coleoidea, 471
 spawning migration
 Ommastrephidae, 533
 spawning response
 Tridacnidae, 333
 spawning season, 23
 Polyplacophora, 173
 spawning seasons, Gastropoda, 591
 speciation
 freshwater gastropods, 746
 species diversity
 Australian pulmonates, 1057
 increase with depth, 40
 species pairs, Triphoridae, 810
 species recognition, Coleoidea, 473
Spectamen, 687
Spectamen philippense, 687
 radula, Fg 15.66
 shell, Fg 15.66
Spengelomenia bathybia
 morphology, Fg 2.2
 Spengel's organs, 639, 642
 Spengler, L., 161
Spengleria, 368, 370
 boring, 368
 in burrow, Fg 8.43
 burrow lining, 368
 distribution, 369, 370
 pedal elevator muscles, 368
 shell, Fg 8.43, 368
 siphons, 368
 sperm bulbs, Ommastrephidae, 532
 sperm morphology, 336
 Anaspidea, 936
 Cephalaspidea, 936
 Heterobranchia, 854
 Mathildidae, 859
 Nudibranchia, 936
 Omalogyridae, 864
 Opisthobranchia, 936
 phylogenetic value, 606
 Scissurellidae, 667
 sperm pouches
 Caenogastropoda, 632
 sperm storage
 Neogastropoda, 587
 Ommastrephidae, 532
 sperm transfer
 Architeuthidae, 528
 Caenogastropoda, 587
 Cephalopoda, 452
 Coleoidea, 469
 Cranchiidae, 540
 Enoploteuthidae, 521
 Galeommatidae, 316
 Loliginidae, 519
 mechanisms, 24
 Octopodidae, 549
 Ocythoidae, 552
 Onychoteuthidae, 524
 pelagic molluscs, 48
 Pulmonata, 590, 1037, 1050
 Sepiidae, 507
 Tremoctopodidae, 551
 Vampyroteuthidae, 543
 spermatogenesis
 Anomalodesmata, 401
 Architectonicidae, 862
 Mactridae, 338
 prosobranchs, 634
 Pulmonata, 1050
 spermatophores, 543, 1106
 Architectonicidae, 862
 Architeuthidae, 528
 Atlantidae, 805
 Carinariidae, 806
 Carinarioida, 804
 Cephalaspidea, 936
 Cephalopoda, 452, 469
 Cerithiidae, Fg 15.82
 Cerithioidea, Fg 15.88, Fg 15.92, 634, 707
 Coleoidea, 501
 Corillidae, 1112
 Cranchiidae, 540
 Cystopeltidae, 1107
 Diastomatidae, 730
 Galeommatidae, 316
 Helicinidae, 702
 Heteropoda, 634
 Histiot euthidae, 529
 Limacina inflata, 24
 Loliginidae, 519
 Mathildidae, 859
 Milacidae, 1103
 Modulidae, 731
 Neritidae, 697
 Neritoidea, 694
 Neritopsina, 634
 Nudibranchia, 936
 Octopodidae, Fg 11.22, 549
 Ocythoidae, 552
 Opisthobranchia, 936
 Phenacolepadidae, 700
 Planaxidae, 724
 Plesiotrochidae, 737
 Potamididae, Fg 15.92
 prosobranchs, 634
 Pulmonata, 1037, 1050
 Pyramidellidae, 867
 Scaliolidae, 733
 Sepiadariidae, 510
 Sepiidae, 507
 Sepiolidae, 511
 Siliquariidae, 720
 Siphonariidae, 1068
 Spirulidae, 504
 Tremoctopodidae, 551
 Turritellidae, Fg 15.88, 716
 Vermetidae, 778–780
 Vermetoidea, 634, 778
 spermatophoric sac
 Coleoidea, 501
 Nautilidae, Fg 12.11
 spermatozogma, 20, 634
 Cerithiopsidae, Fg 1.17
 Epitoniidae, 816
 Janthinidae, Fg 1.17, 814
 pseudocopulation, 816
 Ptenoglossa, 631
 Triphoroidea, 808
 spermatozoa
 Campanilidae, Fg 15.98
 Campaniloidea, Fg 15.98, Fg 15.99
 Cerithioidea, Fg 15.82
 Chaetodermomorphia, 148
 Mactroidea, 337
 Myoidea, 363
 Neomeniomorphia, 148
 Plesiotrochidae, Fg 15.99
 Pulmonata, 1050
 structure, 1050
 taxonomic value, 20
 Turtonidae, Fg 4.19
 Veneridae, Fg 4.19
 spermatozoan dimorphism, 20, 634
 Galeommatidae, 316
 Insecta, 20
 Oligochaeta, 20
 spermatozoan morphology
 Amphibolidae, 1067
 architectonicoid phylogeny, 859
 Hyriidae, Fg 7.5
 Neotrigonia, 292
 Neritidae, 697
 Palaeoheterodonta, Fg 7.5
 Scaphopoda, 436
 Velesunio ambiguus, 292
 spermatozoan ultrastructure
 Amphibolidae, Fg 17.19
 Basommatophora, Fg 17.19
 Camaenidae, Fg 17.19
 Ellobiidae, Fg 17.19
 Helicariionidae, Fg 17.19
 Helicidae, Fg 17.19
 Lymnaeidae, Fg 17.19
 Onchidiidae, Fg 17.19
 Pulmonata, Fg 17.19
 Stylommatophora, Fg 17.19
 Systellommatophora, Fg 17.19
 spermooviduct, Fg 16.18
Sphaeridiotrema globulus, Tb 1.1
 Sphaeriidae, Fg 8.36, Tb 1.4, 352
 family treatment, 355
 gas exchange, 212
 inland waters, 59, 62
Sphaerinova, 82, 355
Sphaerium, 62, 82, 218, 352, 353, 355
 Pleistocene, 353
 Pliocene, 353
 protandry, 215
 shell, 352
 siphons, 355
Sphaerium egregium, 355
Sphaerium tasmanicum
 dispersal by insects, 355
 hinge, Fg 8.36
 shell, Fg 8.36
Sphaerius, 355
Sphaerocylichna, 949
Sphaerodoris incii, 919
Sphaerospira incei, Fg 1.3
Sphaerospira yulei
 sperm ultrastructure, Fg 17.19
Sphenia, 363
 shell, 364
Sphenosolen, Ordovician, Tb 1.6
Sphenotus, Tb 1.6
 Devonian, Tb 1.6, 95
Sphincterochila boissieri
 predation by rodents, 58
Sphincterochila boissieri
 water loss, Tb 17.1
 spicules
 Aplacophora, 145, 146
 Asperspinidae, 960
 Chaetodermatomorpha, 150
 Microhedylidae, 960
 Rhodopemorpha, 960
 spicules, copulatory
 Lepidomeniidae, Fg 2.8
 spindle cowries, Pl 26, 780
 spindle shell, Pl 28
Spiniphiline, 951
Spinospella, 421
 Spionidae, as terebrid prey, 850
 spiral caecum, Fg 15.11
 spiral cleavage, Fg 1.18, 1, 12, 22, 1051
 Bivalvia, 216
 Cephalopoda, 452
 Gastropoda, 591
 Scaphopoda, 436
Spiratella, 981
 as prey of *Clione*, 584
Spiroceras, Silurian, 95
Spiroglyphus, 779
Spirorbis, 779, 996
Spirula, 49, 452, 504, 505, 509, 1017
 external appearance, Fg 11.10
 fin shape, Fg 11.10
 giant fibres, 467
 radula, 500
 salivary glands, 500
 shell, 453, 500
 vertical migration, 471
Spirula australis, 504
Spirula peroni, 504
Spirula peronii, 504
Spirula spirula, 49, 503–505
 distribution, 505
 external appearance, Fg 13.1
 hectocotylus, Fg 13.1
Spirulea prototypus, 504
 Spirulida, 452
 Spirulidae, Fg 11.10, Fg 13.1
 family treatment, 504
Spirulirostra curta
 as fossils, 503
Spissatella, as fossils, 327
Spisula, 337
 density, 41
 as fossils, 339
 on sandy beaches, 37
Spisula austini, 337
Spisula solidissima, 338

INDEX

- Spisula trigonella*, 338
abundance, 338
distribution, 337
hinge, Fg 8.22
shell, Fg 8.22
- Splanchnotrophus elysiae*, 968
- Splendrillia*, 848, 850
- Spondylidae, Fg 4.3, Fg 4.6,
Fg 4.16, Fg 6.19, Pl 12, 278
on reef conglomerate, 36
on reef slope, 35
- Spondylus*, 278, 279
Cretaceous, Tb 1.6
eyes, 18
nervous system, Fg 4.16
statocysts, Fg 4.16
- Spondylus barbatus*, 279
- Spondylus echinatus*, 279
- Spondylus gaderopoides*
Eocene, 279
- Spondylus nicobaricus*, 279
shell, Fg 6.19
- Spondylus sanguineus*, 279
- Spondylus squamosus*, 279
- Spondylus tenellus*, Pl 12
distribution, 279
internal morphology, Fg 6.19
muricid predator, 278
shell, Fg 6.19
- Spondylus varius*, Pl 12
- Spondylus victoriae*, 279
- Spondylus violascens*, 279
- Spondylus wrightianus*, 278, 279
hinge plate, Fg 4.6
shell, Fg 6.19
shell sculpture, Fg 4.3, 199
- sponge fingers, Pl 10, 263
- sponges
as cerithiopsid prey, 811
and Cypraeidae, 782
as dendroderid prey, 1000
as hexabranchid prey, 998
as notaspidean prey, 937
as phyllidiid prey, 1001
as triphoroidean prey, 808
- Spongiobranchaea, 987
- Spongiobranchaea australis*, 987
- Sporadoceras*, Devonian, 95
- Sporadoceras latilobatum*
Devonian, Fg 1.99
- sporozoa
as chiton parasites, 175
parasites of *Lyonsia hyalina*, 402
- Sportella*, 321, 322
external appearance, Fg 8.11
- Sportella jubata*, as fossil, 322
- Sportellidae, Fg 8.11, 318
family treatment, 321
- Spurilla australis*, 1012
- squid fisheries, 74
- squid jigging, 502
- St Paul Island
Argobuccinum pustulosum, 801
- St Vincent Basins, Fg 1.95
- Stabilima*, 268
- Stachella*, Permian, 97
- Standardoceras*, 491
- Stanisic, John, 1039
- Stanley, Capt. Owen, 7
- Staphylea*, 780
- star shells, 675
- starfish, as cardiid predators, 329
- statoconia, 630
Bivalvia, 213
Opisthobranchia, 932
- statocysts, Fg 11.24, Fg 15.18, 453
Anomalodesmata, 401
Bathysciadiidae, 656
- Bivalvia, Fg 4.18, 213
Cavoliniidae, Fg 16.62
- Cephalopoda, 467
- Cocculinoidea, 656
- Cuspidariidae, 401, 425
- echinospira larva, Fg 15.30
- gastropod veliger, 27
- Gastropoda, 630
- Heterodonta, 303
- Laternulidae, 412
- Litiopidae, 715
- Myochamidae, 418
- Octopoda, 468
- Octopodidae, Fg 11.21
- Opisthobranchia, 918, 932
- Osteopeltidae, 663
- Pandoridae, 416
- Pandoroidea, 415
- Parilimyidae, 406
- Patellogastropoda, 642
- Pulmonata, Fg 17.16, 1048
- Scaphopoda, Fg 10.11, 435
- Sepiolidae, Fg 11.21
- structure, Bivalvia, 214
- Vampyromorpha, 468
- Verticordiidae, 421
- Vetigastropoda, 629
- statoliths, Fg 11.21, 630
Bivalvia, 212, 213
cephalopod ageing, 470
Cephalopoda, 467
Opisthobranchia, 932
- Pectinidae, Fg 4.18
- Pulmonata, 1048
- Stearoceras*, 491
- Stegocoelia*, Devonian, 95
- Stellantchasmus aspinosus*, Tb 1.2
- Stellantchasmus falcatus*, Tb 1.2
- Stellaria*, 776
- stellate ganglia
Coleoidea, 466
Teuthoidea, Fg 11.11
- Stenacapha hamiltoni*
radula, Fg 17.10
- Stenocalymma*, type, 439
- stenocalymma larva
Dentaliida, 439
Scaphopoda, 436
- Stenochiton*, 182, 183
habitat, 175
- Stenochiton cymodocealis*, 165, 175
- Stenochiton longicymba*, Pl 7, 165
- Stenoglossa, 582, 606, 620, 703
- Stenogyra*
nervous system, Fg 17.14
- Stenoloron*, Devonian, 95
- Stenomelania*, 82, 729
- Stenoplax heathiana*
embryo, Fg 3.23
- Stenopylis*, 1100
distribution, 1100
diversity, 1100
life span, 1100
- Stenopylis coarctata*, 1100
distribution, 85
habitat, 1100
shell, Fg 17.57
- Stenosemus*, 175
- Stenothecha*, Cambrian, 89
- Stenothyra*, 766
distribution and habitat, 65
diversity in Australia, 766
external appearance, Fg 15.120
as fossils, 766
operculum, Fg 15.120
radula, Fg 15.120
- Stenothyra australis*
shell, Fg 15.120
- Stenothyrella*, as fossils, 766
- Stenothyridae, Fg 15.120, Tb 15.1,
84
in brackish water, 62
family treatment, 765
inland waters, 65
- stenotopy
Aplacophora, 149
- Stephanoceras*, Jurassic, 97
- Stephopoma*
parental care, 637
sperm transfer, 632
- Stephopoma nucleogranosum*
protoconch, Fg 15.89
- Stephopoma roseum*
head-foot, Fg 15.89
radula, Fg 15.89
- stereoglossate radula, 619
- Sthenodonta*, Tb 1.6
- Sthenoteuthis*, 533
light organs, 532
photophores, Fg 11.6
- Sthenoteuthis oualaniensis*
external appearance, Fg 13.22
funnel locking apparatus,
Fg 13.22
hectocotylus, Fg 13.22
- Stichopus mollis*
as tonnid prey, 803
- Sticteulima*, diversity, 817
- Stictodora caballeri*, Tb 1.2
- Stictodora lari*, Tb 1.2
- Stictodora manilensis*, Tb 1.2
- Stilapex*, diversity, 817
- Stilifer*
diversity, 817
feeding, 584
parasitism, 623
- Stilifer inflatus*, shell, Fg 15.154
- Stilifer linckiae*, sex reversal, 633
- Stiliferidae, 817
- Stiliger*, 937, 973, 974
external features, 922
and plastids, 940
- Stiliger boodlea*, Fg 16.19
egg masses, Fg 16.19
- Stiliger cremoniana*, 974
- Stiliger smaragdinus*, Fg 16.55, 938
external appearance, Fg 6.55
- Stiligeridae, relationships, 940
- Stiligerinae, characters, 973
- stimulator
Milacidae, 1103
Veronicellidae, 1049
- Stimulator consetti*
distribution, 63, 84
- Stracolpus atkinsoni*, shell, Fg 14.4
- Stoloteuthis*, 511
- stomach
Anomalodesmata, 399
Arionidae, Fg 14.27
Basommatophora, Fg 14.27
bivalve organisational grades,
209
Buccinidae, Fg 14.25
Caenogastropoda, Fg 14.25
Calliostoma, 618
Clavagellidae, 414
Cocculiniformia, 654
Coleoidea, 500
Conoidea, 847
Donacidae, 346, 347
Ellobiidae, Fg 14.27
Gastrochaenidae, 368
Haminoidae, Fg 14.26
Hyadatinidae, Fg 14.26
lamellibranch, Fg 4.13
Laternulidae, 412
Lymnaeidae, Fg 14.27
Mactridae, 338
Mesodesmatidae, 339
- Myochamidae, 418
- Myoidea, 363, 364
- Pandoridae, 416
- Pandoroidea, 415
- Periplomatidae, 410
- Pholadidae, Fg 8.45
- Planaxidae, Fg 14.25
- Poromyidae, 422
- prosobranchs, 621
- protobranch, Fg 4.13
- Protobranchia, 235
- Psammobiidae, 345
- Pulmonata, Fg 14.27
- structure, Bivalvia, 209
- Tellinidae, 343
- Tellinoidea, 342
- Thyasiridae, Fg 8.5
- Trapeziidae, 349
- Trochidae, Fg 15.11
- Verticordiidae, 399, 421
- Vetigastropoda, Fg 15.11
- Zonitidae, Fg 14.27
- stomach flukes, 67
- stomach types, 324
Anomalodesmata, 399
Bivalvia, Fg 4.13
Chamidae, 309
Cuspidarioidea, 399
Gastrodeuteia, Fg 4.13
Gastropempta, Fg 4.13
Gastropoteia, Fg 4.13
Gastrotiteia, Fg 4.13, 208
Heterodonta, 301, 302
Lucinoidea, 315
Palaeoheterodonta, 290
Poromyidae, 399
Trigoniidae, 296
Ungulinidae, 310
Verticordiidae, 399
- Stomatella*, 671, 684
shell, 685
- Stomatella auricula*, 685
radula, Fg 15.64
shell, Fg 15.64
- Stomatellidae, Fg 14.7
- Stomatellinae, 679
in Australia, 684
description, 684
- Stomatia*, 684
shell, 685
- Stomatia phymotis*, shell, Fg 15.64
- Stomohamites*, Cretaceous, 99
- stony corals
as neomeniomorph prey, 151
- storage techniques, 102
- Stosicia*, distribution, 751
- Stramonita haemastoma*, 823
- Strange, 1038
- Strangesta*
buccal mass, Fg 17.8
carnivory, 58, 1054
egg laying, 1055
external appearance, Fg 17.20,
Fg 17.51
feeding, Fg 17.20, 1054
life span, 1052
oviparity, 1051
radula, Fg 17.51
- Strangesta ramsayi*, Fg 1.65
- Straparollus*, 95
Carboniferous, 95
Devonian, 95
Permian, 97
- Straparollus davidi*
Carboniferous, Fg 1.99
- stratigraphic correlation
Permian, 97
- Strebloceras*, 763
- Streptaxidae, Fg 17.50, Tb 1.5
family treatment, 1090
- Streptaxoidea, description, 1090

- Streptoneura, 568
context of usage, 605
streptoneury, 605
Gastropoda, 576
Opisthobranchia, 918
Streptopinna, 265
as fossils, 267
Streptostele musaecola, shell, 1090
Striacallista, 360
Striarca, 257
Striarca symmetrica, 257
Striarcinae, 257
Striatestea, distribution, 751
Striatocostatum, Cretaceous, 99
Strictispira paxilla
radula, 849
Strictispirinae, 850
Strigilla, 343
Striocadulus, 445
Striopulsellum, 443, 444
strobilation, Cavoliniidae, 980, 982
Strobilopsidae, 1082
Stromatoceras, 491
Strombidae, Fg 1.17, Fg 1.36,
Fg 14.10, Fg 15.121, Pl 25,
Tb 15.1, 13, 766
Aboriginal resources, 36
on coral reefs, 33
family treatment, 766
mating aggregations, 768
ornamentation, 614
prostate gland, 632
on reef flat, 35
Strombina, egg capsules, 829
strombine, Solenoidea, 340
Stromboidae, families, 766
Stromboidea, Tb 15.1
crystalline style, 621
description, 766
locomotion, 612
relationships, 766
Strombus, 766, 768
diversity, 766
features, 766
habitat, 768
locomotion, 574
mating behaviour, 768
shell modification, 572
Strombus aurisdianae, Pl 25
Strombus campbelli
distribution, 768
Strombus canarium
external appearance, Fg 15.121
operculum, Fg 15.121
Strombus denticostatus, 768
Strombus epidromis
shell, Fg 15.121
Strombus gibberulus
radula, Fg 15.121
Strombus gigas, 766, 768
conservation, 115
fishery, 768
mantle cavity, Fg 15.121
Strombus luhuanus, Pl 25
age at maturity, 768
fishery, 768
in middens, Fg 1.36
paraspermatozoa, Fg 1.17
Strombus maculatus
egg mass, Fg 15.121
locomotion, Fg 14.10
Strombus mutabilis
distribution, 768
Strombus raninus, egg mass, 635
Struthiolaria, 768
Struthiolaria papulosa, 768
brooding, 769
burrowing, Fg 15.122
female genital ducts, Fg 15.122
Struthiolariidae, Fg 15.122,
Tb 15.1, 766
endostyle, 616
family treatment, 768
genera, 768
Strzelecki, Paul de, 8
Sturt, Charles, 8
Sturtian fluvifauuna
freshwater molluscs, 81
Sturtian Province, Fg 1.89
Stutchburia,
as fossil, 322
Permian, 97
style sac, 15
Anomalodesmata, 399
Calliostoma, 619
Clavagellidae, 414
Cornirostridae, 856
Galeommatidae, 302
Mactroidea, 302
Pholadidae, Fg 8.45
Solenoidea, 302, 340
Teredinidae, Fg 8.51
Valvatoidea, 856
stylet, Pyramidellidae, 865
Stylidium, 712
Styliferina, veliger, Fg 1.60
Stylocheilus, 937, 976
Stylocheilus longicauda, 941, 977
Stylommatophora, 55, 1047
Australian origins, 1080
description, 1079
as fossils, 1057
molecular sequencing, 1060
pallial configuration, Fg 17.39
phylogeny, 1060
Suavocallia, 705
Subacmea, 639
subantarctic
Ocheyoherpia, 157
Phyllomeniidae, 154
Subinyoites, Triassic, 97
Submantellum, 268
Subninella, 675
Subninella undulata
external appearance, Fg 14.3
suboesophageal lobes
Coleoidea, 466
subpallial cavity, Cocculinidae, 656
subradular organs, 630, 639
Polyplacophora, 171
Vetigastropoda, 629
subradular sense organ, 434
Scaphopoda, 435
substratum grade and molluscs, 41
sub-tentacles, 213
Bivalvia, 213
Subterenochiton, 182
Subterenochiton bednalli, 182
Subterenochiton gabrieli, 182, 183
Subulina octona, Fg 17.22, 1091
Angiostrongylus cantonensis,
1056
shell, Fg 17.47
Subulinidae, Fg 17.14, Fg 17.22,
Fg 17.47, Tb 1.5, 85, 86
family treatment, 1087
Subulites, Devonian, 95
Subvestinautilus, 491
Succinea, 85, 1108, 1109
Succinea australis, Fg 17.66
Succinea norfolkensis
Norfolk Island, 1108
Succinea ovalis
reproductive tract, Fg 17.66
Succinea scalarina, shell, Fg 17.66
Succineidae, Fg 17.66, Tb 1.5, 85
family treatment, 1108
gonoduct fusion, 1049
Succineoidea, description, 1108
Succineoidei, 1086
suckers
Cephalopoda, 454, 457
Octopoda, 545
Octopodidae, 549
Sepioidea, 454, 504
Teuthoidea, 454, 515
Vampyromorpha, 542
suctorial feeding
Cancellariidae, 846
suctorial siphons, 399
Sukashitrochus, 666
Sulcascaris
as pectinid parasites, 277
Sulcascaris sulcata, 262, 265
sulphide oxidase, 243
sulphide oxidation
bacteria, 310, 313
Bathymodiolinae, 251
contribution by partners, 242
and haemoglobin, 313
Lucinidae, 244, 302
Nuculanidae, 240
Solemya reidi, 315
Solemyidae, Fg 5.8, 242
symbiosis with Solemyoidea, 235
Thyasiridae, 302, 315
Sulphur, 7
sulphuric acid and predation, 622
sundial shells, 858
Sunetta, 357, 358, 360
habitat, 358
Sunetta perexcavata, 359
Sunetta vaginalis, 358
Sunettidae, 356
Sunettinae, 356, 358
sunset shells, 345
Supplanaxis, 722, 724
suprabranchial chamber
Bivalvia, Fg 4.5, 203
and brooding, 214
Heterodonta, 303
lamellibranch, Fg 4.5
Lucinidae, Fg 8.3
Nuculoida, Fg 5.1
Pholadidae, Fg 8.45
Protobranchia, Fg 4.5
Solemyoidea, Fg 5.1
Teredinidae, Fg 8.51
Veneroidea, 356
supra-oesophageal lobes
Coleoidea, 466
Surat Basin, Fg 1.95
Surbula, Cretaceous, 353
surf clams, 337
surfers itch, 69
surfing, Dorsaninae, 831
survival without water
Polymesoda erosa, 219
suspension-feeding, 42
adaptations, 585, 623
Arcoidea, 208
Bivalvia, 207
Calyptraeidae, 584
Capulidae, 584
effect of tide, 43
gastropod adaptations, Fg 14.24
Gastropoda, 584
Heterodonta, 209, 302
modifications to ctenidia, 616
Mytilidae, 251
Neomphalidae, 584
prosobranchs, 623
Protobranchia, 208, 235
Pterioidea, 208
Pteriomorpha, 208, 209, 249
Sareptidae, 240
on shelf, 39
Siliquariidae, 718
Solenoidea, 340
Struthiolariidae, 584
Thecosomata, 584
Trochidae, Fg 14.24, 584
Turritellidae, Fg 14.24, 584
Vermetidae, Fg 14.24, 584
Svetlanoceras, Permian, 97
swarming
Atlantidae, 49
Diacavolinia longirostris, 49
Fioloida desmaresti, 49
holoplanktonic molluscs, 49
Limacinidae, 982
Thecosomata, 980
swimmers itch, 64, 69, 721, 724
Cercaria longicauda, 1056
swimming
Akeridae, 975
Aplysia fasciata, Fg 16.9
Aplysiidae, Fg 16.9, 976
Architeuthidae, 528
Bivalvia, 206, 219
Bornella anguilla, 1003
Carinaria mediterranea, Fg 15.5
Carinariidae, 806
Carinarioida, 804
Cavoliniidae, 982
Cephalaspidea, 925
Cirrata, 456
Clione limacina, Fg 16.9
Clionidae, Fg 16.9, 988
Cymbuliidae, 984
Desmopteridae, 985
Dorsaninae, 831
Gastropoteridae, Fg 16.9
Gymnosomata, 986
Hexabranchidae, Fg 16.9, 997
Hexabranchus sanguineus,
Fg 16.9, Fg 16.81
Hydromylidae, 989
Limacina retroversa, Fg 16.9
Limacinidae, Fg 16.9
Limidae, 268
Nudibranchia, 925
Opisthobranchia, Fg 16.9, 574,
925
Opisthotethidae, 545
Ovulidae, 836
Pectinoidea, 206, 219
pelagic nudibranchs, 926
Peraclididae, 983
Pleurobranchidae, Fg 16.9, 979
Pleurobranchus membranaceus,
Fg 16.9
prosobranchs, 606
Sagaminopteron ornatum,
Fg 16.9
Scissurellidae, 666
Scyllaeidae, 1005
Sepiidae, 507
Solemyidae, 241
Solenoidea, 302
Tethyidae, 1006
Triophinae, 994
Umboniinae, 689
Vampyroteuthidae, 542
swimming cycle
Solemyidae, Fg 5.9
Sydaphera, Tertiary, 101
Sydney Basin, Fg 1.95
Sydney rock oyster, Pl 11
fishery, 74
Symbiodinium, 332
symbiont of tridacnid clams, 332
symbiosis
in Aeolidiidae, 939
in Cardiidae, 330, 332
in Fimbridae, 314
in Galeommatoidea, 219
kleptoplasty, 937
in Lucinidae, 313
in Lucinoidea, Fg 8.2
in Nudibranchia, 940
in *Plakobranchus*, 967

INDEX

- in Polyplacophora, 175
in *Pteraeolidia ianthina*, 936
in Sacoglossa, 937, 939, 961
in Solemyidae, 242
in Solemyoidea, 235, 241
in Teredinidae, 302
in Tridacnidae, 302, 332, 333
zooxanthellae, 936
- symbiotic bacteria
Lucinidae, 207
Neogastropoda, 819
Pomatiasidae, 627
scaphopod eggs, 436
Solemyidae, 207
Teredinidae, 209
- sympatry
areas with high levels, 87
Neritidae, 698
- Symphyla, sperm dimorphism, 20
- Synaptocochlea*, distribution, 681
- Synaptorhabda, 225
- Syncyclonema*, Cretaceous, Tb 1.6
- Syncyclonemidae, 275
- synonymy, Architectonicidae, 861
- Synthopsis*, distribution, 811
- Sypharochiton*, 172
- Sypharochiton funereus*, 187
- Sypharochiton pellisserpentis*, 172, 175, 185–187
desiccation, 175
habitat, 175
spawning, 173
- Syphonota*, 976
- Syrinx*, 825
egg capsule, 825
operculum, 825
- Syrinx aruanus*, 832
distribution, 825
operculum, Fg 15.158
radula, Fg 15.158
shell, Fg 15.158
shell size, 569
- Syrioplanorbis*
fossils, 84
as Oligocene fossil, 1058
- Syrioplanorbis hardmani*
as fossil, 1074
- Syrnola*, shell, 867
- Systellommatophora, 55, 1037, 1052, 1067
affinities, 1060
description, 1060
external characters, 1041
- Systrophiidae, 1091
- 
- Taemasotrochus*, Devonian, 95
- Taenioglossa, 620
- taenioglossate radula, Fg 1.14, 582, 620
- taenioid muscle scar
Parilimyidae, 406
- taenioid muscles
Anomalodesmata, 399
Parilimyidae, Fg 9.7, 399
Pholadomyidae, 399
Pholadomyoidea, 406
Verticordiidae, Fg 9.16, 399, 420
Verticordioida, 420
- Tagelus*, ctenidia, 346
- Tagelus californianus*, 346
- Taheitia*, habitat, 758
- Takashia*, 410
- Talabrica*
diversity, 326
as fossils, 327
size, 326
- Tallorbis*, distribution, 681
- Talparia*, 780
- Tamanovalva*, 965, 966
- Tamanovalva babai*, Pl 34
- Tamanovalva limax*, 965, 966
- Tambja*, 994
- Tambja morosa*, radula, Fg 16.76
- Tambja verconis*
external appearance, Fg 16.76
- tanais, as molluscan predators, 39
- Tanaodon*, Devonian, 95
- Tancretella*, Tb 1.6
- Tancretella plana*, Tb 1.6
- Tancretella secunda*, Tb 1.6
- Tanea*, 791
- Taningia*, 516, 523
depth range, 523
external appearance, Fg 11.9
- Taningia danae*, 523
- Tanuella*, Cambrian, 89
- Taoniinae, Fg 13.28, 540
- Taonius*, Fg 11.9, Fg 13.28, 542
- Tapes*
distribution, 360
diversity, 360
habitat, 358, 360
- Tapes dorsatus*, 359
- Tapes philippinarum*, 951
- Tapes semidecussata*
cell count, 210
- Tapetidae, 356
- Tapetinae, 356, 360
- Taphon*, affinities, 832
- Taraninae, 850
- Tasmanian Basin, Fg 1.95
- Tasmaphena sinclairi*
as fossil, 1058
shell, Fg 17.51
- Tasmatica*, 791
- Tate, Prof. Ralph, 10, 101, 196, 236, 301, 432, 1039
- Tatea*, shell, 755
- Tatea huonensis*
operculum, Fg 15.111
- Tatea rufilabris*
Fg 1.48, 63, 83
shell, Fg 15.111
- Tatella*, Cretaceous, Tb 1.6
- Tatella aptiana*, Tb 1.6
- Tatella maranoana*, Tb 1.6
- Taurangia*, Cambrian, 89
- Tauraxinus*, 314
- Tawera*, 357, 358, 360
habitat, 358
- Tawera spissa*
myochamid host, 418
- taxodont condition, evolution, 224
- taxodont dentition
Ctenodontidae, 241
Nuculanoidea, 239
Nuculoida, 235, 237
Solemyoidea, 241
- taxodont system, Fg 4.6
- taxonomy, 343
Achatinellidae, 1080
Ancyliidae, 1071
Buccinidae, 827
Carinarioida, 804
Condylocardiidae, 325
Conoidea, 846
Dialidae, 714
Ellobiidae, 1078
Glacidorbidae, 1075
Hemidonacidae, 331
Hiatellidae, 370
Iravadiidae, 752
Kelliellidae, 350
- Litiopidae, 714
- Lymnaeidae, 1070
- Marginellidae, 838
- Myochamidae, 418
- Neilonellidae, 239
- Noetiidae, 257
- Nuculanoidea, 239
- Omalogyroidea, 864
- Pandoridae, 415
- Philobryidae, 260
- Physidae, 1074
- Planorbidae, 1072
- Pupillidae, 1082
- Rhytididae, 1091
- Sareptidae, 240
- Sepiidae, 505
- Solenoida, 341
- Succineidae, 1108
- Succineoidea, 1108
- Thiaridae, 727, 729
- Triphoridae, 810
- Trochoidea, 671
- Unionoida, 289
- Vermetidae, 779
- techniques
collecting, 101
fixation, 102
molecular, 103
preservation, 102
quantitative ecology, 104
storage, 102
- Technophorus*, Ordovician, 93
- Tectarius*, 738, 739
- Tectarius rusticus*, 739
- Tecticrater*, 658
- Tecticrater compressa*, 659
shell, Fg 15.45
- Tectisumen*, 658
- Tectisumen clypidellaeformis*, 658, 661
shell, Fg 15.45
- Tectonatica*, 791
- Tectus*, shell, 683
- Tectus pyramis*, radula, Fg 15.63
- Tegula*, 612
- Tegula funebris*, 582
- Tegulaherpia*, 153
Bass Strait, 153
external features, Fg 2.8
- Tegulaplax*, 187
- Tegulinae, 679
- Teichertia*, 493
- Teichertia prora*, Fg 12.10
- Teicherticeras desideratus*
Devonian, Fg 1.98
- Teiichispira*, 92
- Teiichispira cornucopiae*, Fg 1.98
- Teinostoma*, 765
- Teinostoma lucida*
shell, Fg 15.119
- Teinostoma sensu lato*, 765
- teleoconch
Campanilidae, Fg 15.98
Opisthobranchia, 915
- teleplanic larvae, 39, 52
- Caenogastropoda, 637
- Ranellidae, 800
- Telescopium*, 724
as fossils, 727
habitat, 726
- Telescopium telescopium*, Fg 1.47, 726
habitat, 726
radula, Fg 15.93
shell, Fg 15.92
- Tellidorella*, distribution, 325
- Tellina*, 343
Cretaceous, Tb 1.6
shell/body relationship, Fg 4.10
- Tellina alternata*, haemoglobin, 212
- Tellina australis*, distribution, 343
- Tellina botanica*, endemic, 343
- Tellina buttoni*, density, 344
- Tellina capsoides*, distribution, 343
- Tellina chloroleuca*
distribution, 343
shell, Fg 8.28
- Tellina cockburnensis*
biomass, 304
density, 344
- Tellina deltoidalis*
endemic, 343
shell, Fg 8.28
- Tellina fabula*, 343
- Tellina foliacea*, distribution, 343
- Tellina imbellis*, endemic, 343
- Tellina inflata*, distribution, 343
- Tellina margaritina*, endemic, 343
- Tellina mariae*, 304, 343
- Tellina ovalis*, distribution, 343
- Tellina pharaonis*, Pl 15
- Tellina scobinata*, 343
distribution, 343
shell, Fg 8.28
- Tellina tenuis*, 342, 343
filtration rate, 343
- Tellina virgata*, distribution, 343
- Tellinidae, Fg 4.10, Fg 8.27, Fg 8.28, Pl 15, 343
on coral reefs, 34
estuarine distribution, 41
family treatment, 343
as prey of commercial fishes, 344
on reef flat, 35
on sand plains, 38
- Tellininae, 343
- Tellinoidea, 342
description, 342
families, 343
origin, 342
- Tellinopsis*, Silurian, Tb 1.6
- tellins, 343
- Temnocinclinae, 666
- Temnodiscus*, Devonian, 95
- Tenagodus*, Fg 15.89, 718, 720
locomotion and shape, 575
- Tenagodus anguina*, 720
- Tenagodus australis*, 720
shell, Fg 14.4
- Tenagodus cumingii*, 720
- Tenagodus nucleogranosum*, 720
- Tenagodus pennatum*, 720
- Tenagodus ponderosa*, 720
- Tenagodus roseum*, 720
- Tenagodus (Stephopoma)*, Fg 15.89, 718, 720
- Tenagodus tricuspe*, 720
- Tenagodus weldii*, 720
- Tenellia pallida*, 936
- Tenison Woods, J.E., 101, 196, 236
- tent shells, 675
- tentacles, Fg 11.24, 295, 494
Anomalodesmata, 401
Cephalopoda, 453
Chiroteuthidae, 533
Coleoidea, 499
Grimalditeuthidae, 538
Joubiniteuthidae, 539
Limidae, Fg 4.22
Mastigoteuthidae, 537
musculature in cephalopods, 454
Nautilidae, Fg 12.11
Nautiloidea, 454
Ommastrephidae, 532
Opisthobranchia, 932
Pulmonata, 1048
Sepiadariidae, 509
Sepiidae, 505
Sepioidea, 454, 504

- Spirulidae, 504
 Teuthoidea, 454, 515
 Trigonidae, 290
 tentacular club
 Architeuthidae, 527
 Bathyteuthidae, Fg 13.19, 530
 Brachyteuthidae, 532
 Chiroteuthidae, 533
 Cranchiidae, 539
 Ctenopterygidae, 530
 Cycloteuthidae, 525
 Enoplateuthidae, 521
 Histioeuthidae, 528
 Idiosepiidae, 514
 Joubiniteuthidae, 539
 Lepidoteuthidae, 526
 Loliginidae, 517
 Octopoteuthidae, 523
 Ommastrephidae, 532
 Onychoteuthidae, 523
 Sepiolidae, Fg 13.7, 510, 511
 Teuthoidea, Fg 13.19
 Thysanoteuthidae, 533
 tentacular structure
 Athyrocaporidae, 1109
Tentaoculus, 662
Tentaoculus haptricola
 protoconch, Fg 15.47
 shell, Fg 15.45, 663
Tentidonax veruinus
 distribution, 347
Terebellum, 766
 penis, 768
Terebellum terebellum
 burrowing, 766
 distribution, 766
 shell, Fg 15.121
Terebra, 576, 850
 alimentary tract, 850
 characters, 850
 diversity, 851
 enteropneust prey, 850
 habitat, 850
 locomotion and shape, 575
 predatory attack frequency, 851
 protection, 851
 shell modification, 572
Terebra addita
 endemic, 851
Terebra albida, 851
Terebra amanda, shell, Fg 15.175
Terebra areolata
 alimentary tract, 850
Terebra assecla, endemic, 851
Terebra babylonica
 alimentary tract, 850
Terebra bicolor, endemic, 851
Terebra bratcheri, endemic, 851
Terebra brazieri, endemic, 851
Terebra chlorata, shell, Fg 15.175
Terebra crakei, endemic, 851
Terebra crenulata
 alimentary tract, 850
 shell, Fg 15.175
Terebra dimidiata
 alimentary tract, 850
 columnellar folds, Fg 14.12
 foregut, Fg 15.175
 shell, Fg 14.12
Terebra flindersi, endemic, 851
Terebra gouldi
 alimentary tract, 850
 copulation, 850
Terebra guttata
 alimentary tract, 850
Terebra inconspicuus
 endemic, 851
Terebra jacksoniana, endemic, 851
Terebra kieneri, endemic, 851
Terebra lima, shell, Fg 15.175
Terebra maculata, Fg 1.38
 alimentary tract, 850
Terebra marrowae, endemic, 851
Terebra praelongus, endemic, 851
Terebra russetae, endemic, 851
Terebra scalariformis
 endemic, 851
Terebra subulata
 alimentary tract, 850
Terebra trilineata, endemic, 851
Terebra tristis, endemic, 851
Terebra ustulata, endemic, 851
Terebra vallesia, endemic, 851
Terebra venilla, endemic, 851
Terebra walkeri, 851
Terebralia, 724, 726, 727
 as fossils, 727
 in mangroves, 45
Terebralia palustris, Pl 24, 726
 habitat, 726
 operculum, Fg 15.92
 radula, 726
 shell, Fg 15.92
Terebralia semistriata, 726
 habitat, 726
Terebralia sulcata, 726
 egg mass, Fg 15.92
 habitat, 726
 radula, Fg 15.93
 spermatophore, Fg 15.92
 Terebridae, Fg 1.38, Fg 14.12,
 Fg 15.176, Tb 15.1, 847
 attack by *Calappa*, 851
 on coral reefs, 33
 family treatment, 850
 foregut, Fg 15.175
 genera, 850
 locomotor wave form, 612
 on reef slope, 35
 on sand plains, 38
 shells, Fg 15.175
 Terebridae 14.11, 575
 Teredinidae, Fgs 8.51–8.54, Pl 16,
 371
 cues for settlement, 54
 economic importance, 76
 family treatment, 376
 in mangroves, 45
 on reef slope, 35
 subfamilies, 378
Teredo
 habitat, 374
 hermaphroditism, 23
 larviparity, 374, 378
 reproduction, 303
Teredo bartschi, Fg 8.53
Teredo clappi, Fg 8.53
Teredo furcifera, Fg 8.53
Teredo mindanensis, Fg 8.53
Teredo navalis, Fg 8.53
Teredo poculifer, Fg 8.53
Teredo triangularis, Fg 8.53
Teredonavalis, shell, 199
Teredora
 ctenidia, 376
 habitat, 378
Teredora malleolus, 376
Teredora princesae, shell, Fg 8.52
Teredothyra, habitat, 378
Teredothyra dominensis, Fg 8.53
Teredothyra matacotana, Fg 8.53
Terenolla, characters, 850
 Tergipedidae, Fg 16.11, Fg 922,
 Fgs 16.18–16.20, Pl 36
 cerata, Fg 16.20
 cnidosac, Fg 16.20
 defensive glands, Fg 16.20
 development, Fg 16.19
 family treatment, 1016
 jaw plate, Fg 16.11
 terminology
 adductor muscle, 199
 adductor muscle scars, Fg 4.10,
 Fg 4.11
 bivalve ctenidia, 208
 hinge dentition, Fg 4.6, 200
 ligament, 199
 muscle scars, 199
 periostracum, 201
 valve, 198
 Terquemiidae, 273
 terrestrial exploration, Mollusca, 8
 terrestrial Mollusca
 adaptations, 606
 Australian families, Tb 1.5
 conservation, 107
 distribution and affinities, 85
 origins, 606
 origins and affinities, 87
 range size, 87
 territoriality
 Octopodidae, 473
 Patellogastropoda, 642
 Tertiary, 99, 752, 755, 816
 Acteonidae, 944
 Angariinae, 675
 Anomalodesmata, 404
 Arctidae, 348
 Australian pulmonates, 1058
 Basommatophora, 1067
 Bithyniidae, 761
 Bivalvia, 222, 223
 Calliostomatinae, 686
 Calyptraeidae, 774
 Camaenidae, Fg 17.24
 Cancellariidae, 846
 Capulidae, 775
 Cardiidae, 223, 328
 Cerithiidae, 712
 Cerithioidea, 708
 Cerithiopsidae, 811
 Chamoidea, 307
 Cleidothaeridae, 420
 Cocculiniformia, 654
 Columbellidae, 827
 Conidae, 854
 Conoidea, 847
 Corbulidae, 366
 Costellariidae, 845
 Crassatellidae, 306, 326
 Cuspidariidae, 425
 Cyamiidae, 318
 Cypraeidae, 784
 Dorsaninae, 830
 Eucyclinae, 682
 Eulimidae, 817
 Fascioliidae, 833
 fossil molluscs, Fg 1.101
 Gastropoda, 95
 Glossidae, 351
 Haminoeidae, 955
 Harpidae, 838
 Hemidonacidae, 328
 Hiattelloidea, 370
 Hyriidae, 298
 Iravadiidae, 752
 Juliidae, 965
 Limidae, 268
 Marginellidae, 841
 marine transgressions, 91
 Melongeninae, 832
 Myochamidae, 405
 Nassariidae, 831
 Nautilus, 495
 Neoleptonidae, 318
 Neotrigonia, 293
 Patellogastropoda, 645
 Pinnidae, 267
 Planorbidae, 1058, 1074
 Potamididae, 727
 Pyramidellidae, 867
 Retusidae, 950
 Ringiculidae, 946
 Rissoidea, 751
 Seguenziidae, 693
 Skeneidae, 691
 Solariellinae, 688
 Strombidae, 768
 Succineidae, 1109
 Terebridae, 851
 Thraciidae, 405, 409
 Tricoliinae, 678
 Tridacnidae, 336
 Trigonidae, 293, 296
 Triphoridae, 811
 Triviidae, 788
 Trochidae, 680
 Trochinae, 683
 Trochoidea, 673
 Umboniinae, 690
 Vanikoridae, 772
 Veneridae, 360
 Vermetidae, 780
 Verticordiidae, 422
 Vitrinellidae, 765
 Volutidae, 835
Tesseracme, 439
Tesseracme quadrapicale
 shell, Fg 10.14
Tesseropora rosea, 31
 mortality from limpets, 30
Testacella, 1108
 diet, 584
 function of radular teeth, 583
Testacella haliotidea, 55, 1108
 carnivory, 58
 external appearance, Fg 17.65
 radula, Fg 17.65
 reproductive tract, Fg 17.65
 as snail predator, 1056
Testacellidae, Fg 17.65, Tb 1.5,
 1102
 as earthworm predators, 1107
 family treatment, 1107
 testis
 Coleoidea, 501
 Nautilidae, Fg 12.11
Testudinalia, 652
 Tethyan affinities
 Cardiidae, 331
 Trigonidae, 293
 Tethyan distributions
 Patellogastropoda, 644
 Tethyidae, Fg 16.17, Fg 16.19,
 Fg 16.92, Pl 36
 diet, 938
 egg mass, Fg 16.19
 family treatment, 1005
 rhizophore, Fg 16.17
 Tethyidae, 1005
Tethys, 1005, 1006
 Tethys Sea
 campaniloidean radiation, 733
 northern Australian bivalves, 222
Tethys vagina
 as host to *Ocythoe*, 552
 Tetrabranchiata, 452
 tetracycline as a marker, 514
 tetrataxic waves, Pulmonata, 1041
 tetradotoxin, Coleoidea, 500
Tetronychoteuthis, 526
Tetronychoteuthis dussumieri, 526
 external appearance, Fg 13.16
 skin tubercles, Fg 13.16
Tetronychoteuthis massyae, 526
 tubercles, 526
Teudopsis, as fossils, 517
Teuthrostris, 656
Teuthrostris cancellata, 656
 beaks as food, 656
 Teuthoidea, 452
 description, 515
Teuthowenia megalops, 540

INDEX

- Teuthowenia pellucida*, Pl 2, 540, 542
egg mass, 540
external appearance, Fg 13.28
ontogenetic descent, 51
sperm transfer, 540
- Thaidinae, 822
and predation, 699
- Thais*, 822, 823
fishery, 823
as fossils, 824
- Thais orbita*,
as bioindicator, 76
distribution, 593
imposex, 76
- Thala*, use of poison, 844
- Thala floridana*, 843
- Thalassoceras*, Permian, 97
- Thalassocyron*, 797, 798
operculum, 799
- Thalassocyron bonus*
distribution, 798
operculum, 798
radula, Fg 15.138
- Thalassocyronidae, 798
- Thalotia conica*, radula, Fg 15.63
- Thatcheriinae, 850
- threatened species
Placostylus bivaricosus, 114
- Theba*
aestivation, 1113
agricultural pest, 71
- Theba pisana*, Fg 1.77, 85
aestivating animals, Fg 17.71
external appearance, Fg 17.71
as pests, 71, 1114
- Thecacera*, 993
- Thecacera pacifica*, Fg 16.74
radula, Fg 16.74
- Thecacera pennigera*, Fg 16.17,
Fg 16.74, 941, 993
external appearance, Fg 16.74
introduction, 940
rhinophores, Fg 16.17
- Thecalia*, incubation, 324
- Thecosomata, 980
and dinoflagellate toxins, 980
external features, 923
feeding, 926
in food webs, 980
as hydrological indicators, 49
locomotion, 13
spermatophores, 936
- Themapupa adelaidae*
thermoregulation, 1055
- Theodoxus*
excretory system, Fg 15.16
feeding, 697
genital ducts, Fg 15.22
as parasite host, 694
prostate gland, 632
reproduction, 697
- Theodoxus fluvialilis*, 620, 697
development, 697
effects of pollution, 700
euspermatozoa, Fg 1.17, 697
morphology, Fg 15.73
paraspermatozoa, 697
- Theodoxus oualanensis*, 695
- Theora*, 344
- Theora fragilis*, as fish prey, 344
- Theora lubrica*
ecology, 344
as fish prey, 344
- Theridium*, as fossils, 712
- thermal limits, *Nautilus*, 494
- thermoregulation
Neritidae, 697
Pulmonata, 1055
in terrestrial molluscs, Fg 1.63, 56
- Thestylea*, diversity, 239
- Thetis*, 10, 196, 236
- Thiara*, Tb 1.2, 65, 82, 729
host of *Trichobilharzia* sp., 69
in mound springs, 64
parthenogenesis, 588
- Thiara amarula*
alimentary tract, Fg 15.94
distribution, 82
mantle cavity, Fg 15.94
radula, Fg 15.94
shell, Fg 15.94
- Thiara balonnensis*
distribution, 65, 82, 729
parthenogenesis, 23, 729
shell, Fg 15.94
- Thiara lirata*, distribution, 82
- Thiara scabra*, 727
as parasite host, 728
- Thiaridae, Fg 1.73, Fg 15.94,
Tb 1.4, Tb 15.1
affinities, 709, 727, 729, 730
as disease vectors, 65
family treatment, 727
inland waters, 62, 65
as parasite hosts, 727
parthenogenesis, 19, 65
polyphyly, 729
schistosome hosts, 68
taxonomic status, 107
- Thiarinae, characters, 727
- Thiele, Johannes, 145, 639
classification, 566, 606
- Thliptodon*, 989
- Thliptodontinae, 988
- Thomson, Prof. Charles, 8
- Thoralidae
as fossils, 237
- Thoralus cranchii*, 514
- Thorunna*, Fg 16.10, 1000
radular teeth, Fg 16.10
- Thracia*, 397, 408
as fossils, 405
orientation, 408
- Thracia alciopae*, 409
- Thracia conradi*, 408
- Thracia meridionalis*
distribution, 409
- Thracia ovalis*, shell, Fg 9.8
- Thracia persacrosa*
as fossils, 405
- Thracidora*, 408, 421
diversity, 409
- Thracidora arenosa*
distribution, 422
- Thracidora flindersi*
distribution, 422
- Thraciidae, Fg 9.8
family treatment, 408
- Thracioidea, 226
description, 407
families, 407
- Thraciopsis*, 408, 409
diversity, 409
ligament, 409
secondary hinge teeth, 398
- threatened taxa
conservation, 107
Coxiella striata, 112
Hydrobiidae, 64
Hyridella glenelgensis, 61
Notopala hanleyi, 707
Notopala sublineata, 707
Viviparidae, 707
- threatening processes
in conservation, 107
- Thularion*, distribution, 1106
- Thunnus alalunga*, 552
- Thunnus thunnus*, 552
- Thuridilla*, Fg 16.48, 966–968
external appearance, Fg 16.48
- Thuridilla bayeri*, 968
- Thuridilla caerulea*, 968
- Thuridilla gracilis*, 968
- Thuridilla ratna*, 968
- Thuridilla splendens*, 968
- Thyasira*, Cainozoic, 314
- Thyasira adelaideana*, 314
- Thyasira flexuosa*, 314, 315
internal morphology, Fg 8.5
shell, Fg 8.5
- Thyasiridae, Fg 8.2, Fg 8.5, 309,
310
family treatment, 314
- Thyca*, 775
diversity, 817
feeding, 584
shell, 817
- Thyphorellidae, 1102
- Thysanodontinae, 679, 687
- Thysanophora*
shell encrustation, 571
- Thysanoteuthidae, Fg 11.10,
Fg 13.23, 533
family treatment, 533
- Thysanoteuthis*, 533
- Thysanoteuthis rhombus*, 533
external appearance, Fg 11.10,
Fg 13.23
fecundity, 469
fin shape, Fg 11.10
funnel locking cartilage, Fg 13.23
radula, Fg 13.23, 533
school size, 533
- Tibia*, habitat, 766
- Tibialectus*, boring, 253
- tidal elevation
effects on molluscs, 42
- Tihkia*, Triassic, 97
- Timanites*, Devonian, 95
- Timoclea*, 358, 360
habitat, 358
- Tindaria*, 237
- Tindaria calistiformis*
life span, 218
- Titanoceras*, 491
- Titiscania*, 614
- Titiscania limacina*, 694, 700
in Australia, 700
external appearance, Fg 15.75
habitat, 701
reproductive system, Fg 15.75
- Titiscaniidae, Fg 15.75, Tb 15.1,
610, 693, 694
family treatment, 700
- Tivela*, 357, 360
nymph, 356
- Tivela stultorum*,
eggs, 216
sexual expression, 215
- Tobinian fluvifaunula
freshwater molluscs, 81
- Tobinian Province, Fg 1.89
- Todarodes*, colouration, 532
- Todarodes angolensis*
distribution, 533
- Todarodes filippovae*
beak, Fg 11.25
distribution, 533
- Todarodes pacificus*, 49, 476
distribution, 533
external appearance, Fg 13.22
fishery, 476
hectocotylus, Fg 13.22
- Todarodinae, 532
- Todaropsis*, colouration, 532
- Todaropsis eblanae*
distribution, 533
external appearance, Fg 13.22
hectocotylus, Fg 13.22
- toheroa, 339, 340
- Toledonia*, 947, 948
- Toledonia limnaeoides*, 948
- Toledonia succinaeformis*, 948
- Tolgachloritis jacksoni*
shell sculpture, Fg 17.3
- Tolmachovia*, Ordovician, 93
- Tolmaia*, Tb 1.6
- Tomichia*, 83
habitat, 756
- Tomthompsonia*, 979, 980
- Tomthompsonia antarctica*, 980
- Tomura*, 856
- Tonicia*, 187
- Tonicia fortilirata*, 187
- Tonicia lamellosa*, 187
- Tonicia (Lucilina)*, 187
- Toniciinae, 185
- Tonna*, 793, 797, 798, 802, 803
foot, 803
as fossils, 803
habitat, 803
proboscis, 793
protoconch, 803
- Tonna cerevisina*
preying on *Stichopus mollis*, 803
shell, Fg 15.144
- Tonna chinensis*, external
appearance, Fg 15.144
- Tonna galea*, radula, Fg 15.144
- Tonna perdix*, 803
as holothurian predator, 803
prey capture, Fg 14.23
- Tonna zonata*
feeding, Fg 15.144
as holothurian predator, 803
- Tonnidae, Fg 14.23, Fg 15.144,
Tb 15.1, 792
family treatment, 802
- Tonnoidea, 819
acid secretion, 622
boring, 622
description, 792
echinoderms as prey, 622
families, 792
- Toorna*, 1016
- tooth plates
Acmaeidae, 648
Nacella, 647
Nacellidae, 646
- tooth shells, 431
- tooth systems, Heterodonta, Fg 4.6
- toothed pearl oysters, 225, 264
- top shells, 680, 683
- Toralimysia*, 315
- Torellia*
diversity in Australia, 774
- Torinista*, 861
diversity, 861
- Tomatellinidae, 1080
- Tornatellinops*, 1080, 1081
shell, 1080
viviparity, 1080
- Tornatellinops jacksonensis*
shell, Fg 17.40
- Tornatellinops variabilis*
radula, Fg 17.40
reproductive tract, Fg 17.40
- Tornatina*, 948–951
shell, Fg 16.27
- Tornatina apicina*, 949
- Tornatina apiculata*, Fg 16.27, 949
external appearance, Fg 16.27
shell, Fg 16.27

- Tornatina canaliculata*, Fg 16.14
gizzard plates, Fg 16.14
Tornatina candei, Fg 16.4,
Fg 16.10
radular teeth, Fg 16.10
shell, Fg 16.4
Tornatina hofmani, 949
Tornatina sp., Fg 16.27
Tornidae, 763
Torr, William George, 10, 163, 568
Torres Strait
dispersal path, 85
effect of closure, 77
Torresitrachia torresiana
habitat, 1052
shell, Fg 14.4, Fg 17.69, 1112
torsion, 25
adaptive significance, 605
functional significance, 565
Gastropoda, Fg 14.2, 18, 565
and mid-oesophagus, 618
Opisthobranchia, 929
organisational effects, 605
and streptoneury, 605
in veliger, 22
toxins
blue-ringed octopus, 549
octopodid salivary glands, 549
saliva in Bursidae, 586
saliva in Cymatiidae, 586
Toxoceratoides
Cretaceous, 99
Toxoglossa, 620, 703, 819, 846
toxoglossans as predators, 583
toxoglossate radula, Fg 1.14, 582,
819
Conoidea, 846
evolution, 849
trace elements, nautiloid ratios, 486
Tracheophilus sisowi, Tb 1.1
Tracheopulmonata, 1047, 1108
Trachiopsis
habitat, 1052
Trachysmatidae, 692
Trachyteuthis, Cretaceous, 99
Transennella
brooding, 356
byssal gland, 356
distribution, 360
habitat, 360
teeth, 356
Transenpitar, habitat, 360
transport of live pulmonates, 1059
transverse adductor muscle
Volvatellidae, 962
Trapania, 991, 992
Trapania aureopunctata, Fg 16.10
radula, Fg 16.10
Trapania brunnea, 941
Trapania japonica, Fg 16.72
external appearance, Fg 16.72
radula, Fg 16.72
Trapeziidae, Fg 4.12, Fg 8.33, 348
family treatment, 348
Trapezium, 348, 349
shell, 349
Trapezium bicarinatum
habitat, 349
Trapezium obesa, habitat, 349
Trapezium oblongum
internal morphology, Fg 8.33
shell, Fg 8.33
Trapezium sublaevigatum
habitat, 349
Tremadocian, 93
Tremanotus, Devonian, 95
tremata, 668
Haliotidae, 571, 667
Pleuromarioidea, 664
Trematoda
Australian hosts, Tb 1.1
Austrobilharzia terrigalensis, 721
Clonorchis sinensis, 760
Corbiculidae as vectors, 355
as parasites of hyriids, 61
Planaxis sulcatus, 724
in pterotracheids, 808
in thiarids, 727
in viviparids, 707
Tremoctopodidae, Fg 11.25,
Fg 13.36, 551
family treatment, 551
Tremoctopus, 551
autotomy, 551
diet, 551
sperm transfer, 469
use of *Physalia*, 51, 551
Tremoctopus gelatus
distribution, 552
Tremoctopus violaceus, 551–552
beak, Fg 11.25
hectocotylus, Fg 13.36
radula, Fg 13.36, 551
sexual dimorphism, Fg 13.36
Triaphorus, as fossil, 322
Triassic, 97, 269, 278, 671
Arctidae, 348
Aviculopectinoidea, 275
Bakevelliidae, 265
Calliostomatinae, 686
Cardiidae, 328, 336
Cardioidea, 328
Cenoceras, 491
Cuspidariidae, 425
Cuspidarioidea, 424
Dicerocardiidae, 351
Dimyidae, 274
fossil molluscs, Fg 1.100
Gryphaeinae, 269
Halobioidea, 268
Hyriidae, 298
Laternulidae, 412
Limidae, 268
Lophinae, 272
marine transgressions, 91
Mysidiellidae, 250
Naticidae, 792
Nautilidae, 493
Neritidae, 700
Ostreidae, 270
Ostreina, 268
Ostreoida, 269
Pectinoidea, 275
Pleuromariidae, 666
Plicatulidae, 273
Plicatuloidea, 273
Pteriidae, 262
Scaphopoda, 437
Scissurellidae, 667
Tellinoidea, 343
Veneroida, 306
trialism, Opisthobranchia, 932
Triboniophorus
distribution, 1109
feeding, 1054
radula, 1109
Triboniophorus graeffei, Fg 1.61,
Pl 32, 1109
distribution, 1109
external appearance, Fg 17.67
jaw, Fg 17.67
microhabitat, 1052
radula, Fg 17.67
reproductive tract, Fg 17.67
ureter, 1109
tributyltin, effects on molluscs, 76
Trichobilharzia in ducks, 69
Tricholiinae in Australia, 673
Trichomya
endemism, 253
as fossil, 223
Miocene, 253
Trichomya hirsutus, 223
shell sculpture, 199
Trichoplax, 960
Trichotropidae, 772, 774, 798
Trichotropis, 774, 775
sex reversal, 633
shell, 774
Trichotropis borealis
external appearance, Fg 15.127
eye, Fg 15.19
sex reversal, 633
Trichotropis cancellata, 774
Tricolia, 677, 678
in Australia, 677
distribution, 678
habitat, 672
Tricolia fordiana, radula, Fg 15.59
Tricolia gabiniana
distribution, 678
Tricolia rosea, distribution, 678
Tricolia tomlini, 677
distribution, 678
Tricolia variabilis, 677, 678
head-foot, Fg 15.59
radula, Fg 15.59, 677
sexual dimorphism, 677
shell, Fg 15.59
Tricoliinae, description, 677
Tricola
as host to *Schistosoma*, 756
Triculinae, locomotion, 755
Tridachia, 967
Tridachiella, 967
Tridacna, 16, 55, 332, 333, 336
amoebocytes, 210
ancestry, 336
conservation, 115
ctenidia, 332
digestive rhythm, 209
excretory system, 211
generic characters, 332
hyaline organs, 332
life span, 218
mantle, 332
mariculture, Fg 1, 83
pallial eyes, Fg 4.17
Permian, 97
pyramidellid parasitism, 867
sensu lato, 332
sensu stricto, 332
Tridacna (Chametrachea), 333, 336
habit, 332
Tridacna crocea, Pl 14, 332, 335
boring, 304, 335
shell, Fg 8.19
status, 115
Tridacna derasa, 305, 332, 335,
336
abundance, 335
depths, 335
mariculture, 75
shell, Fg 8.20
Tridacna gigas, 35, 218, 224, 303,
305, 332, 333, 335, 336
abundance, 335
age at maturity, 335
ctenidia, 332
fecundity, 335
internal morphology, Fg 8.18
kidney, 303
mariculture, Fg 8.18, 75, 336
on reef slope, 35
shell, Fg 8.18, Fg 8.19
shell size, 199
shell weight, 333
size, 217
spawning, Pl 14
Tridacna maxima, Pl 14, 218, 332,
335, 336
distribution, 335
shell, Fg 8.19
shell form, Fg 4.2, 199
status, 115
Tridacna (Persikima), 332
Tridacna rosewateri, 332, 333
Tridacna squamosa, 332, 336
distribution, 335
shell, Fg 8.19
Tridacna tevorora, 332, 333
depths, 335
Tridacnidae, Fg 1.32, Fg 1.82,
Fg 4.2, Fg 4.18, Fg 4.22,
Fgs 8.18–8.20, Pl 14, 16, 73,
332
Aboriginal resources, 72
affinities, 332, 336
ancestry, 336
conservation, 115
on coral reefs, 33
drying meat, Fg 1.82
economic importance, 75
family treatment, 332
hatcheries, 75
illegal fishing, 114
mariculture, Fg 1.83, 75
on reef conglomerate, 36
on reef slope, 35
Tridacnoidea, Fg 8.19
characters, 332
description, 332
Tridentifera, 744
Triforidae, 808
Triforinae, 811
Triforis
diversity, 811
protoconch, 811
radula, 811
siphonal notch, 811
Triforis dexta
distribution, 811
Triforis epallaxa
distribution, 811
Triganglionata, 854
relationships, 606
status, 567
Triganochlamydidae, 1102
Trigonia, Tb 1.6, 7, 295, 296
Cretaceous, Tb 1.6
as fossil, 296
Jurassic, 97
sensu stricto, 293
Trigoniidae, Fg 1.86, Fg 4.6,
Fg 4.9, Fg 7.7, Fg 7.8,
Fgs 7.1–7.5, 226
affinities, 294
distribution of species, Fg 1.86
family treatment, 295
fossil record, 293
use in jewellery, 293
Trigoniocardia, 331
Trigoniocardia media, 331
Trigonioida, 226, 289
characters, 294
distribution, 293
families, 295
Trigonioida
affinities with Unionoidea, 293
description, 295
mantle lobes, 204
Trigonoceroidea, 491
Trigonostoma, distribution, 846
Trigonostoma scalare
radula, Fg 15.172
shell, Fg 15.172
Trigonostoma scalariformis
proboscis, Fg 15.172
Trigonucula, Triassic, 97
Trimusculidae, Fg 17.38, 1047
family treatment, 1079
Trimusculoidea, description, 1078
Trimusculus, 1079

INDEX

- Trimusculus conica*, 1079
radula 17.38, 1078
reproductive system, Fg 17.38
shell, Fg 17.38
- Trimusculus reticulatus*, 1079
- Trinchesia*, 1016
- Triopha*, 993
- Triophidae, status, 993
- Triophinae, 993
bioluminescence, 994
characters, 993
external appearance, Fg 16.75
- Triphora*, use of proboscis, 622
- Triphora contrerasi*
female genital duct, Fg 15.149
- Triphoridae, Fg 14.36, Fg 15.148,
Fg 15.149, Tb 15.1, 708
classification, 566
family treatment, 809
sinistral whorls, 809
species pairs, 810
- Triphorinae, 810
- Triphoroidea, Tb 15.1, 703, 808
affinities, 808
characters, 808
description, 808
and Janthinoidea, 610
- Trippa intacta*, Fg 16.82
radula, Fg 16.82
- Tripsycha*, 779
- Trisidos*,
burrowing, 254
ciliary tracts, Fg 4.12
habitat, 256
heart, 256
hinge, 254
sculpture, 254
shell, 254
- Trisidos tortuosa*, shell, Fg 6.2
- Trisidos yongei*, 254
- Tristan da Cunha
Argobuccinum pustulosum, 801
- triton shells, 799
- Tritonia*, 1001
ciliary locomotion, 574
organisation, Fg 16.1
- Tritonia gombergi*, Fg 16.17
rhinophores, Fg 16.17
- Tritoniidae, Fg 16.16, Fg 16.17,
Fg 16.86, Pl 36
diet, 938
family treatment, 1002
- Tritoniopsis*, 1002
- Tritoniopsis elegans*, Fg 16.86
external appearance, Fg 16.86
- Tritonoharpa*, diversity, 846
- Tritonoharpa ponderi*
shell, Fg 15.172
- Triton's trumpet, 801
- Trivia*, 632, 787, 790
development, 787
egg capsule, 635, 636
egg laying, 787
larval shell, 787
mantle, 787
radular function, 583
shell muscles, 613
use of proboscis, 622
- Trivia arctica*, 787
- Trivia calvaricola*
radula, Fg 15.132
- Trivia merces*, distribution, 787
- Trivia monacha*, 787
anatomy, Fg 15.132
echinospira larva, Fg 15.132
egg capsules, 787
egg laying, Fg 15.24
genital ducts, Fg 15.22
- Trivia pellucidula*
reproductive system, Fg 15.132
- trivias, 786
- Triviidae, Fg 15.24, Fg 15.132,
Pl 26, Tb 15.1, 774, 786
family treatment, 787
- Triviinae, 787
- Trochaclidinae, 679
- Trochidae, Fg 1.25, Fg 1.42,
Fg 14.15, Fg 14.24,
Fg 14.28, Fg 15.3, Fg 15.8,
Fg 15.10, Fg 15.11,
Fg 15.15, Fgs 15.18–15.22,
Fgs 15.61–15.68, Pl 23,
Tb 15.1, 605
in Australia, 672
Australian taxa, 679
family treatment, 679
gut, morphology, Fg 15.10
locomotor wave form, 611
on reef crest, 35
on rocky shores, 29
on sand plains, 38
in seagrass, 38
shell cleaning, 613
shell collecting, 76
spawning, 631
- Trochidobia*, 63
radiation, 64
- Trochinae, 679
description, 683
taxonomy, 683
- Trochini, 683
- Trochocerithium*, 735
- Trochoidea, Tb 15.1, 664
in Australia, 671
circulation, 624
description, 671
diversity in New Zealand, 673
features, 610
fertilisation, 631
heart, 623
mantle cavity, Fg 15.7
nephridial gland, 626
phylogeny, 672
respiratory flow, 616
and Seguenzoidea, 610
spiral caecum, 621
- Trocholites*, 491
- Trochomorpha melvillensis*, 1104,
1105
distribution, 85
habitat, 1105
radula, Fg 17.62
reproductive tract, Fg 17.62
shell, Fg 17.62
- Trochomorphidae, Fg 17.62,
Tb 1.5, Tb 17.4, 1102
family treatment, 1104
- Trochonema*
Devonian, 95
Ordovician, 93
- trochophore, 12
Archaeogastropoda, 22
Bivalvia, 25, 216
Gastropoda, Fg 14.34, 591
Golfingiidae, Fg 1.1
Heterodonta, 303
Ostreidae, Fg 4.19
Patellidae, Fg 1.1, Fg 14.34
Patellogastropoda, 22, 25
Phyllocodidae, Fg 1.1
Polyplacophora, Fg 3.25, 25, 173
relationship with other phyla, 1
Scaphopoda, 25
Sipuncula, Fg 1.1
structure, 591
Vetigastropoda, 22, 25
- Trochostilifer*, diversity, 817
- Trochus*, 572
distribution, 683
illegal fishing, 114
in middens, 672
shell, 683
- Trochus intextus*, radula, Fg 15.63
- Trochus niloticus*
exploitation, 115
fishery, Fg 1.84, 75, 672, 683
shell, Fg 15.63
- trochus shell, 680, 683
economic importance, 76
fishery, 75, 683
- Tropaeum*, Cretaceous, 99
- trophic group amensalism, 42
- trophic transfer, Bivalvia, 219
- Trophon*, 823
- Trophoninae, 822
- Trophonopsis*, 823
- Tropical Australian Province, 78
- Tropidodiscus*
Devonian, 95
Silurian, 95
- Tropidomya*, hinge teeth, 424
- trough shells, 337
- Truncatella*, 758
- Truncatella cylindrica*
head-foot, Fg 15.114
- Truncatella scalarina*
radula, Fg 15.114
shell, Fg 15.114
shell modification, Fg 14.6
- Truncatellidae, Fg 14.6, Fg 15.114,
Tb 15.1, 606
affinities, 755
family treatment, 758
locomotor wave form, 611
loss of apex, 572
- Truncatelloidea, 566, 745, 746
- Tryblidiida, 3
- trypsin, 236
- Tuarangia*, 223
- tuatua, 340
- Tubastraea*, 938, 1016
as prey of *Phestilla melanobranchia*, Fg 16.107
- Tubbreva*, 741
distribution, 743
- tube, Clavagellidae, 413
- tubercles
Lepidoteuthidae, Fg 13.16, 526
Mastigoteuthidae, 538
- Tubularia*, as flabellinid prey, 1012
- Tucetona*, 260
as fossils, 260
sculpture, 259
- Tucetona auriflua*, 259
distribution, 260
internal morphology, Fg 6.6
- Tucetona broadfooti*, endemic, 260
- Tucetona flabellata*, endemic, 260
- Tucetona gunyoungensis*
Tertiary, Fg 1.101
- Tucetona hoylei*, shell, Fg 6.6
- Tudicla*, Tertiary, 101
- Tudiclinae, 825
- Tudivasum armigera*
operculum, Fg 15.663
radula, Fg 15.663
shell, Fg 15.663
- Tugali*, 669
- Tugonia*, 363, 364
shell, 364
- Tugonia inopinata*, 364
- Tularia*, 941, 1012
- tun shells, 802
- tunas, as carinariid predators, 806
- unicates
as ranellid prey, 800
as velutinoidean prey, 786
- turban shells, 675
fishery, 76
- Turbinaria*, 948
- Turbinella*
egg capsule, 825
operculum, 825
- Turbinellidae, Fg 15.158, Tb 15.1
family treatment, 824
subfamilies, 825
- Turbinellinae, 825
- Turbinidae, Fg 1.46, Fg 14.3,
Fgs 15.55–15.60, Tb 15.1
family treatment, 673
ornamentation, soft substrata, 614
on reef crest, 35
- Turbininae
in Australia, 673
description, 675
in middens, 676
- Turbo*, 6, 675
distribution, 676
Jurassic, 97
oogenesis, 24
- Turbo fluctuosus*
head-foot, Fg 15.57
- Turbo jourdani*, Fg 1.46
- Turbo marmoratus*
conservation, 115
fishery, 676
- Turbo petholatus*
use in jewellery, 676
- Turbo smaragdus*, radula, Fg 15.57
- Turbo torquatus*, 676
distribution, 78, 593
external appearance, Fg 14.3
shell, Fg 15.57
- Turbo undulatus*
breeding season, 24
commensalism, 32
fishery, 76, 676
- Turbonellina*, Devonian, 95
- Turbonilla*
distribution, 867
shell, 867
- Turricula nelliae*
feeding, 850
prey capture, 850
radula, 850
- Turriculinae
Australian genera, 850
- Turridae, Fg 1.17, Fg 14.23,
Fg 15.174, Fg 15.175,
Tb 15.1, 633
diversity and latitude, 850
external appearance, Fg 15.174
family treatment, 847
foregut, Fg 15.175
veliger shell, Fg 15.174
- Turritiles*, 99
- Turrinae
Australian subfamilies, 850
- Turritella*, 816
euspermatozoa, Fg 15.88
suspension-feeding, 585
- Turritella communis*, 716, 718
behaviour, Fg 15.88
external appearance, Fg 15.88
morphology, Fg 15.88
spermatophore, Fg 15.88
- Turritella terebra*, 716
suspension-feeding, Fg 14.24
shell, Fg 15.88
- Turritellidae, Fg 14.4, Fg 14.24,
Fg 15.88, Tb 15.1
affinities, 718, 720, 732
characters, 716
endostyle, 616
family treatment, 716
locomotor wave form, 612
sperm transfer, 632
suspension-feeding, 623

Turritellinae, 718
 Turritellopsinae, 718
Turriopsis truncatus, prey, 508, 519
 turtles
 as carinariid predators, 804, 806
Turtonia
 egg capsule, Fg 4.19, 216
 spermatozoa, Fg 4.19
Turtonia minuta
 distribution, 356
 egg capsules, 216
Turtoniidae, Fg 4.19, 305, 356
 tusk shells, 431
Tutufa, 793, 794
 jaw plates, 793
 opercular nucleus, 794
Tutufa bardeyi, shell, 794
Tutufa bufo, 794
Tutufa oyamai, radula, Fg 15.136
Tutufa rubeta, 794
 aperture, 793
 mantle cavity, Fg 15.136
Tylodina, 932, 934, 937, 940,
 977-979
 external features, 922
Tylodina alfredensis, 978
Tylodina americana, 978
Tylodina corticalis, Fg 16.58, 977,
 978
 external appearance, Fg 16.58
Tylodina fungina, 978
Tylodina perversa, 978
Tylodinae, Fg 16.58
 family treatment, 977
Tylodinoidea, characters, 977
Tylospira, 768
 Tertiary, 101
Tylospira coronata
 Tertiary, Fg 1.101
Tylospira scutulata, 768
 habitat, 768
 operculum, Fg 15.122
 radula, Fg 15.122
 shell, Fg 15.122, 768
Tylothea, 848
 type localities, Pulmonata, 1038
Typhis
 diversity in Australia, 823
 as fossils, 824
Typhis philippensis
 shell, Fg 15.156
 typhlosoles, Fg 15.11
Calliostoma, 619
 typical sperm, 634
 Typinae, 822
 Tyrian purple, Muricidae, 823



Uca, 45
Udotea, 970
Ulrichospira, Devonian, 95
 ultrafiltration, Bivalvia, 211
Ulva, 864, 960
Ulva lactuca, 722
Umbilia, 780, 784
 as fossils, 784
Umbilia eximia, fossil, 594
 umbo
 Bivalvia, Fg 4.4, 198
 Chamidae, Fg 8.1
 curvature, 198
 Veneridae, Fg 4.4
Umboniidae, 689

Umboniinae, 679, 688
 suspension-feeding, 616
 in Australia, 689
 characters, 689
 description, 689
Umboniini, 689
 shell, 689
Umbonium, 623
 on sand plains, 38
 shell, 689
 suspension-feeding, 585, 623
Umbonium moniliferum
 head-foot, Fg 15.68
Umbonium vestiarius
 feeding, 689
 neck lobe, Fg 15.68
 shell, Fg 15.68
Umbotropis, Devonian, 95
Umbraculidae, Fg 16.59, 940
 family treatment, 978
Umbraculum, 932, 934, 937,
 977-979
 external appearance, 922
 radula, 926
Umbraculum umbraculum,
 Fg 16.58, 941, 978, 979
 external appearance, Fg 16.59
 umbrella species, 106
Umburra cinefacta
 Silurian, Fg 1.98, 95
Unctidae, Norfolk Island, 114
Undulomya, Permian, 97
Ungulinidae, Fg 4.2, Fg 8.6, 309
 family treatment, 315
Unio, 289, 296
 Triassic, 97
Unionella, Triassic, 97
Unionicolidae
 as hyriid parasites, 61
Unionidae, Fg 4.21, 22, 59, 226,
 296
 brooding, 25
 Cretaceous, 99
 fossil fauna, 59
 Mesozoic fossils, 88
Unionoidea, 226, 289
 description, 296
Unionoidea, 226
 description, 296
 families, 296
 fossil record, 294
Univalvia, 3
Uperotus, 378
 ctenidia, 376
 habitat, 378
Uperotus clavus
 shell, Fg 8.52
Uraloceras, Permian, 97
Uranie, 162, 196, 568, 1038
Urciolaria korscheltii, 175
Urechis caupo, 364
 ureotely, 16
 Polyplacophora, 169
 ureter, 1085, 1106, 1107, 1109
 Achatinellidae, 1080
 Achatinelloidea, 1080
 Amimopina macleayi, Fg 17.12
 Basommatophora, 1045
 Camaenoidea, 1112
 Cionelloidea, 1081
 Enidae, 1080
 Helicoidea, 1113
 Mesurethra, 1046
 Orthurethra, 1046
 Partuloidea, 1085
 Pulmonata, Fg 17.12, 1045
 Pupilloidea, 1082
 Sigmurethra, 1046, 1086
 Stylommatophora, 1045
 Succineoidea, 1108
 Testacellidae, 1107

uric acid excretion
 Pulmonata on land, 56, 1045
 uricotelly, 16
 Stylommatophora, 1046
 urine, *Calliostoma*, 626
Urocyclidae, 1102
Urosalpinx, 622
Urosalpinx cinerea
 boring, 622
 habitat, 823
Urospora, 972
Uroteuthis, shell, 517



Vacunella, as fossils, 406
Vacunella curvata, as fossils, 405
Vacunella waterhousei
 Permian, Fg 1.99, 89
Vaginulidae, 1065
Vaginulus plebeius,
 distribution, 1065
 external appearance, Fg 17.28
 origin, 1065
 penis, Fg 17.28
 vector, *Angiostrongylus*
 cantonensis, 1056
Valavata, egg capsules, 856
Valdivia, 145, 452
Vallatotheca, Devonian, 95
Vallisneria spiralis
 association with *Ferrissia*, 63
Vallonia costata, 1085
 reproductive tract, Fg 17.44
Vallonia pulchella, 1085
 jaw, 1084
 radula, Fg 17.44
 shell, Fg 17.44, 1084
Valloniidae, Fg 17.44, Tb 1.5, 1082
 family treatment, 1084
Valonia, 970, 974
Valvatidae, 856
 ancestry, 856
 hermaphroditism, 633
Valvatoidea, Tb 15.1, 854
 characters, 854
 description, 854
 families, 856
 relationships, 606
 valve dentition
 Nuculidae, Fg 5.2
 Solemyidae, Fg 5.2
 valve of Leiblein
 Cancellariidae, 846
 Columbellidae, 829
 Costellariidae, Fg 15.171
 function, 622
 Marginellidae, Fg 15.168, 839
 Muricidae, 822
 Muricoidea, Fg 15.155
 Neogastropoda, Fg 15.155,
 Fg 15.168, Fg 15.170,
 Fg 15.171, 610, 819
 Turbinellidae, 825
 Volutomitridae, Fg 15.170
 valves
 Bivalvia, 195
 circulation, Fg 4.15
 sculpture, Fg 3.3
 structure, Fg 3.4
 terminology, 198
Vampyromorpha, 452
 description, 542
Vampyroteuthidae, Fg 11.10,
 Fg 11.14, Fg 13.30, 543
 family treatment, 542
Vampyroteuthis, 454, 467, 468, 501
 alimentary tract, Fg 11.14

arms, 454
 coelom, 457
 external appearance, Fg 11.10
 fin shape, Fg 11.10
 frontal/vertical lobe system, 466
 locomotion, 457
 prey detection, 458
 reproduction, 468
 statocyst, 468
 suckers, 454
Vampyroteuthis infernalis, 499,
 542-543
 brain, 543
 external appearance, Fg 13.30
 eyes, 543
 ontogenetic ascent, 51
 phylogeny, 543
 radula, Fg 13.30
 reproduction, 543
 Van Roosenbergh, exploration, 6
 Vancouver, Capt. George, 195
Vanikoridae, Fg 15.124, Tb 15.1,
 714, 769, 771
 affinities, 703
 family treatment, 771
Vanikoro, 771, 772
 diversity in Australia, 772
Vanikoro cancellata, 772
 head-foot, Fg 15.124
 radula, Fg 15.124
 shell, Fg 15.629
Vanikoro helicoidea, 772
Vanikoroidea, 771
Vanikoroidea, Tb 15.1
 description, 769
 families, 769
Vanikoropsis
 Cretaceous, 99
Vanikoropsis jacki
 Cretaceous, Fg 1.100
Varicopeza, 712
 habitat, 709, 712
Varicopeza pauxilla, habitat, 712
Varicorbula, shell, 366
Varicorbula gibba, 366
 crystalline style, 366
 internal morphology, Fg 8.42
 pseudofaeces, 366
 siphons, Fg 8.42
Varohadra, 81
 vascular system
 Caenogastropoda, Fg 15.15
 Haliotidae, Fg 15.15
 Trochidae, Fg 15.8, Fg 15.15
 Vetigastropoda, Fg 15.8,
 Fg 15.15
 Vasiniae, 825
Vasum
 distribution, 825
 egg capsules, 825
Vasum ceramicum
 distribution, 825
 operculum, Fg 15.158
 radula, Fg 15.158
 shell, Fg 15.158
Vasum flindersi
 distribution, 825
Vasum turbinellum
 distribution, 825
Vaucheria, 974
Vaucheria vipera, 971
Vayssiorea, 996
Vayssiorea caledonica, 996
 external appearance, Fg 16.80
Vayssiorea felis, 996
 radula, Fg 16.80
Vayssioreidae, Fg 16.80, 990
 family treatment, 996
Velacumantus, 721
Velella spp., 46, 48, 49, 1015, 1017
 as janthinid prey, 814

INDEX

- Veella veella*, Fg 1.49
- Velepallina*, 705, 706
shell, 705
- Velepallina beddomei*
distribution, 706
habitat, 706
shell, Fg 15.80
- Velepallina strangei*
distribution, 706
habitat, 706
shell, Fg 15.80
- Vesunio*, 59
acrosome ultrastructure, Fg 7.5
distribution, 82, 298
glochidium, 59
in Jardinian fluvifauna, 81
in Leichhardtian fluvifauna, 81
in Lessonian fluvifauna, 81
- Vesunio ambiguus*, 60, 61, 293, 298
Aboriginal resources, 72, 293
age at maturity, 298
as bioindicator, 60, 293, 298
breeding season, 293, 298
development, 293
glochidium larva, Fg 7.6
habitat preferences, 59, 60
hinge plate, Fg 4.6
limiting factors, 60
in Michellian fluvifauna, 81
pearls, 297
reproductive timing, 24
resistance to desiccation, 60
shell, Fg 7.9, 60
spermatozoa, 292
- Vesunio angasi*, Fg 1.68, 60, 298
distribution, 59
habitat, 59
population dynamics, 61
shell form, Fg 1.67, 60
- Vesunio moretonicus*, 298
- Vesunio sentaniensis*
in Gaimardian fluvifauna, 81
- Vesunio wilsonii*, 59, 298
desiccation, 293
distribution, 59
habitat, 59
in Sturtian fluvifauna, 81
- Vesunioninae*, 59, 293
- veliconchas
Anomalodesmata, Fg 9.4
Conidae, 853
Pandoridae, Fg 9.4
- veliger, 12
Architectonicidae, 862
Atlantidae, Fg 15.145
Bivalvia, 216
Caenogastropoda, 637
Carinarioidea, Fg 15.145
Cavoliniidae, Pl 34
characteristics, 25, 51
Cypraeidae, Fg 15.130
Cypraeoidea, Fg 15.130
dispersal, 592
Epitoniidae, Fg 15.152
feeding, 592
food selection, 52
Gastropoda, Fg 14.35, 590–592
Heterodonta, 303
hinge structure, 52
Janthinoidea, Fg 15.152
lecithotrophy, 590
metamorphosis, 638
morphological development, 638
Muricidae, Fg 14.35
Nassariidae, Fg 1.55, 52
Neritidae, Fg 15.73
Neritopsina, Fg 15.73
Opisthobranchia, 27, 590
Pinnidae, Fg 1.57
planktonic life span, 592
planktotrophy, 590
settlement cues, 638
- veliger morphology, 27, 591
Caenogastropoda, Fg 15.29
Nassariidae, Fg 15.29
Neogastropoda, Fg 15.29
Ostreidae, Fg 4.20
- Velutina*, 632, 786, 789, 790
development, 787
egg capsule, 635
gamete production, 633
hermaphroditism, 789
shell, 789
shell muscles, 613
use of proboscis, 622
- Velutinae*, Fg 14.7, Fg 15.30, Fg 15.133, Tb 15.1, 774
family treatment, 789
- Velutinae*, 787
- Velutinoidea*, Tb 15.1, 819
description, 786
- Venericardia*, Tb 1.6
- Venericardia bimaculata*
habitat, 304
- '*Venericardia*' *cavatica*
distribution, 324
- '*Venericardia*' *quoyi*, 323
distribution, 324
- '*Venericardia*' *rosulenta*
distribution, 324
internal morphology, Fg 8.12
- Veneridae*, Fg 1.7, Fg 1.86, Fg 4.6, Fg 4.9, Fg 4.12, Fg 4.19, Fg 8.37, Fg 8.38, Fgs 4.1–4.4, 356
on coral reefs, 34
estuarine distribution, 41
family treatment, 356
on reef flat, 35
on sand plains, 38
shore zonation, Fg 1.45
subfamilies, 356
- Venerinae*, 356, 358
- Veneroidea*, 226, 306
description, 306
superfamilies, 306
- Veneroidea*, 355
description, 355
families, 356
- Venerupis*, 360, 361
byssal gland, 356
distribution, 360
diversity, 360
habitat, 360
nestling, 358, 360
- Venerupis crenata*
shell sculpture, Fg 4.3, 199
- venom
Cephalopoda, 459
Incirrata, 458
Octopoda, 459
- venom apparatus
Conoidea, 846, 847
- venom gland, Conidae, 852
- venous system
Cephalopoda, 461
Nautiloidea, 488
- ventilating behaviour
Solemyidae, Fg 5.10
- ventilation rate, *Nautilus*, 464
- Ventomnestia*, 954, 955
- ventral groove
Neomeniomorpha, 145
- ventricle, Bivalvia, Fg 4.15
- Ventricularia*, 358
- Venus*, 356
eulatero-frontal cilia, Fg 4.12
lateral teeth, 358
spermatozoa, Fg 4.19
- venus ears, 667
- Venus mercenaria*, development, 54
- Vepricardium*, 331
- Vepricardium multispinosum*
shell, Fg 8.15
shell sculpture, Fg 4.3
- Verco, Sir Joseph, 10, 163, 196, 432, 568
- Vercomaris*, distribution, 846
- Verconia*, 941, 1000
- Verconia verconis*, 938
external appearance, Fg 14.8
- Vercularion*, oviparity, 1051
- Veremolpa*, Tertiary, 101
- Vermetidae*, Fg 15.129, Pl 24, Tb 15.1, 585, 632, 708
affinities, 718, 779
colonial life, 779
coral reef infauna, 35
family treatment, 779
genera, 779
as muricid prey, 823
relationships, 779
sperm transfer, 632
suspension-feeding, 623
- Vermetoidea*, Tb 15.1
description, 778
- Vermetus*, 779, 780
operculum, 779
- Vermicularia*, 716, 718, 779
affinities, 718
shell, 718
- Vermicularia spirata*, 716
mantle cavity, Fg 15.88
- Vermiculariinae*, 718
- Veronicellacea*, 1064
- Veronicellidae*, Fg 17.22, Fg 17.28, Tb 1.5, 1039, 1064
family treatment, 1065
nematode vectors, 1067
pest species, 1067
ureter, 1045
- Vertambitus*, 421
- vertical migration
Brachioteuthidae, 532
Cephalopoda, 51, 471
Chiroteuthidae, 537
Enoploteuthidae, 521
Histiototeuthidae, 530
Lepidoteuthidae, 526
Lycoteuthidae, 520
Mastigoteuthidae, 538
Ommastrephidae, 532
Pterotracheidae, 807
Sepiidae, 508
Spirulidae, 505
Thecosomata, 980
- Verticordia*, 405, 420, 421
Eocene, 405
Tertiary, 405
- Verticordia bordaensis*
distribution, 422
- Verticordia erica*
distribution, 421
shell, Fg 9.16, 421
- Verticordia jaffaensis*, 420
distribution, 421
- Verticordia tasmanica*
distribution, 422
- Verticordiidae*, Fg 9.1, Fg 9.5, Fg 9.16, 399
family treatment, 420
- Verticordioidae*, 226
description, 420
- Vertiginidae*, Tb 1.5
- Vertigininae*, distribution, 1084
- Vertisphaera*, 421
- Vesicomya*, 350
- Vesicomya sensu stricto*, 350
- Vesicomyacidae*, 350
- Vesicomyidae*, 305, 348
family treatment, 350
- Veteranella (Glyptoleda)*
as fossils, 240
- Vetigastropoda*, Tb 14.1, Tb 15.1, 567, 605, 606, 631, 637
ancestral mantle cavity, Fg 15.7
apomorphies, 664
circulation pattern, 623
circulatory system, 624
component groups, 610
description, 664
ect-aquasperm, 20
effects of torsion, 605
euspermatozoa, modified, 20
eyes, 629
fertilisation, 631
heart, 623
internal morphology, Fg 15.3
kidney asymmetry, 625
kidney function, 625
nervous system, 628
oesophageal glands, 618, 621
organisation, 605
osphradium, 630
pallial organs, 615
papillary sac, 626
podocytes, 627
primitive features, 605
respiratory flow, 616
sensory organs, 629
sensory papillae, 630
shell muscles, 613
shell structure, 614
sperm morphology, 634
status, 567
stomach, 621
superfamilies, 664
- Vexillidae*, 841
- Vexillinae*, 843
- Vexillum*, 843–845
habitat, 844
prey capture, 844
- Vexillum bernhardina*
shell, Fg 15.171
- Vexillum (Costellaria)*
as fossils, 845
habitat, 844
- Vexillum luculentum*
radular teeth, Fg 15.171
- Vexillum patriarchalis*
radular teeth, Fg 15.171
- Vexillum plicarium*
morphology, Fg 15.171
- Vexillum (Pusia)*, habitat, 844
- Vexillum rugosum*
radular teeth, Fg 15.171
shell, Fg 15.171
- Victaphanta*
affinities, 1093
radula, Fg 17.51
- Victaphanta atramentaria*
external appearance, Fg 17.51
reproductive tract, Fg 17.51
- Victaphanta compacta*, Pl 31
- Victodrobia*, 83
affinities, 755
- Victoria River Basin, Fg 1.95
- Vincennes*, 920
- violet snails, 813
- Virgatospinctes*, Jurassic, 97
- Virgus*
in Riechian fluvifauna, 81
- virus diseases
transmission by molluscs, 72
- visceral loop, Gastropoda, 576
- visceral nerve chain
pulmonate groupings, 1047
- visceral nerve loop, 930
- Visceroconcha, characters, 3
- visceropallium
Cephalopoda, 451
Gastropoda, 565

- vitellogenesis, Scaphopoda, 436
- Vitreledonella richardi*, 547
- external appearance, Fg 13.34
- radula, Fg 13.34, 547
- Vitreledonellidae, Fg 13.34, 547
- family treatment, 547
- Vitreobalcis*, diversity, 817
- Vitreolina*
- foot, 817
- head protection, 817
- Vitreolina philippii*
- external appearance, Fg 15.154
- Vitrinella*, 765
- Vitrinellidae, Fg 15.119, Tb 15.1, 746, 772
- hermaphroditism, 633
- family treatment, 763
- Viviparidae, Fg 15.81, Tb 1.4, Tb 15.1, 82, 706
- declines in Murray River, 107
- in freshwater, 62
- inland waters, 65
- suspension-feeding, 623
- taxonomic status, 107
- as trematode hosts, 707
- Viviparinae, 706
- viviparity
- Achatinellidae, 1080
- Achatinelloidea, 1080
- Cavoliniidae, 982
- Cerithioidea, 708
- endemism, 707
- Glacidorbidae, 1038, 1075
- Janthinidae, 814
- Ocythoidae, 552
- Philobryidae, 260
- Pulmonata, 1038
- Pupilloidea, 1082
- Stylommatophora, 1050
- Thecosomata, 980
- Vitreledonellidae, 547
- Viviparus*, 627
- kidney primordai, 627
- nephridial gland, 626
- nervous system, Fg 15.17
- ovoviviparity, 637
- Vlaminghian fluvifaunula
- freshwater molluscs, 81
- Vlaminghian Province, Fg 1.89
- Volegalea*, 832
- Volegalea wardiana*, 832
- Volema*, distribution, 832
- Volupicuna*, 325
- Voluta*, dispersal, 592
- Voluta maculata*, 6
- Voluta musica*
- digestive system, Fg 15.164
- Volutacea, 819
- volutes, 833
- Volutidae, Fg 1.6, Fg 1.20, Fg 14.23, Fg 15.164, Pl 28, Tb 15.1
- on coral reefs, 33
- exploitation threat, 36
- family treatment, 833
- fossil description, 594
- gene flow, 592
- on reef flat, 35
- on reef slope, 35
- regional variation, 36
- on sand plains, 38
- shell collecting, 76, 115
- Volutoconus*
- distribution, 835
- as fossils, 835
- Volutomitra*, 843
- radula, 842
- Volutomitra fragillima*
- radula, Fg 15.170
- Volutomitridae, Fg 15.170, Tb 15.1
- family treatment, 842
- prostate gland, 632
- Volutopsiinae, 827
- Volva*, 784
- Volva haynesi*, Fg 15.131
- Volva nectarea*, shell, Fg 15.131
- Volva volva*, 784
- host, 786
- shell, Fg 15.131
- Volvarina*, 841
- Volvarina taeniolata*
- mantle cavity, Fg 15.168
- proboscis, Fg 15.168
- Volvarinella cairoma*
- external appearance, Fg 14.7
- Volvatella*, 932, 940, 962, 963, 966
- Volvatella bermudae*, 963
- Volvatella cincta*, 963
- Volvatella kawamurai*, 963
- Volvatella pyriformis*, 963
- Volvatella ventricosa*, 963
- Volvatella vigourouxii*, Fg 16.44
- external view, Fg 16.44
- shell, Fg 16.44
- Volvatellidae*, Fg 16.44
- family treatment, 962
- Volviniae*, 784
- genera, 784
- Volvulella*, 949, 950
- Volvulella rostrata*, Fg 16.28
- external appearance, Fg 16.28
- shell, Fg 16.28
- Vulcanomya*, hinge teeth, 424
- vulnerable species, 106
- Vulsella*, 264
- as fossils, 264
- habitat, 263
- Vulsella laevigata*, 264
- Vulsella spongiarum*, Pl 10
- density, 263
- distribution, 262
- and *Dysidea*, 263
- shell, Fg 6.9
- Vulsellidae*, 262
- 
- Wadeoceras*, 491
- Waimatea*, 843
- Waimatea obscura*, 843
- Wallace, Alfred Russell, 77
- Walloway Basin, Fg 1.95
- Wallucina*, 311
- Wanganella*, shell, 691
- Wanwania*, Ordovician, 93
- Cambrian, 92
- warm temperate fauna, 593
- warragará, Teredinidae, 371
- Warrana*, 350
- wart organs, 639, 642
- Warthia*, Permian, 97
- Warthia intermedia*
- Permian, Fg 1.99
- Watasenia scintillans*
- trawl catches, 523
- water balance
- Ampullariidae, 627
- Pulmonata, 1055
- role of kidneys, 56
- in terrestrial molluscs, 16, 55
- Viviparus*, 627
- water conservation
- Pulmonata, Tb 17.1, 581, 1045, 1055
- Pupillidae, 1082
- semi-slugs, 1055
- slugs, 1055
- Subulinidae, 1087
- water flow
- in generalised bivalve, Fg 4.12
- water loss,
- Patella*, 625
- pulmonates on land, Tb 17.1
- water resorption
- Stylommatophora, 1046
- water vascular system
- Naticidae, 790
- Waterhouse, Frederick, 8, 9
- watering pot shells, 397, 412
- Watson, R. Boog, 431
- wave form, locomotion, 612
- web-feeding
- Cavoliniidae, 982
- Cymbuliidae, 984
- Peraclididae, 983
- Thecosomata, 980
- wedge clams, 339
- wedge shells, 347
- weed itch, 69
- Weinkauffia*, 954, 955
- Wemersoniella*, 445
- Wemersoniellidae
- family treatment, 445
- wentletraps, Pl 24, 42, 814
- Westracystis*, radiation, 86
- Westracystis lissus*, life span, 1052
- Westraltrachia*, feeding, 1054
- Westraltrachia froggatti*
- shell, Fg 17.69, 1112
- Westraltrachia instita*
- radula, Fg 17.69
- Westraltrachia porcata*
- radula, Fg 17.69
- Westraltrachia subtila*
- radula, Fg 17.69
- Westralunio*
- distribution, 82, 298
- glochidium, 59
- in Riechian fluvifaunula, 81
- Westralunio carteri*, 81, 298
- distribution, 59
- effect of salinisation, 61
- in Vlaminghian fluvifaunula, 81
- whale bones
- as food, 656
- as osteopeltid food, 663
- as substratum, 658
- wheel shells, 673
- whip squids, Fg 13.25, 38
- wide-mouths, 684
- Wilhelminaia mathildae*
- distribution, 85
- Wilkes, Capt. Charles, 7
- Willan, Richard C., 920
- Williamsoceras*
- arterial system, Fg 12.5
- infula, 488
- Willochra Basin, Fg 1.95
- wing plate
- Desmopteridae, Fg 16.65
- wing shells, 261, 265
- winged oysters, 261
- wings
- Cymbuliidae, 984
- Hydromylidae, 989
- Limacinidae, 981
- Peraclididae, 983
- winkles, 738
- Wiso Basin, Fg 1.95
- Witchellia*, Jurassic, 97
- Woods, Tenison, 10
- Woodsella*, Cretaceous, 99
- Woolnoughia*, Permian, 97
- Worthenia*, Carboniferous, 95
- Worthoceras*, Cretaceous, 99
- Wutinoceras*, 490
- 
- Xanthomelon*, 81
- shell, 1112
- Xanthomelon obliquirugosum*, shell, Fg 17.69
- Xanthomelon pachystylum*
- water conservation, 1055
- Xanthomelontidae, 86
- Xenodonta*, 656
- Xenodonta bogasoni*, 653
- Xenogalea*, 795
- Xenophalium*, 795
- Xenophora*, 776, 778
- Cretaceous, 99
- diversity, 776
- encrustation of shell, 571
- as fossils, 778
- Tertiary, 101
- Xenophora cerea*, 776
- Xenophora conchyliophora*, 776, 778
- feeding, 776
- Xenophora exuta*, feeding, 776
- Xenophora flindersi*
- development, 776
- distribution, 778
- operculum, Fg 15.128
- Xenophora gigantea*, 776
- Xenophora indica*, 776
- head-foot, Fg 15.128
- operculum, Fg 15.128
- shell, Fg 15.128
- Xenophora mekranensis*, 776
- Xenophora neozelanica*, 776
- anatomy, Fg 15.128
- protoconch, Fg 15.128
- Xenophora pallidula*, 776
- operculum, Fg 15.128
- Xenophora peroniana*, 778
- distribution, 778
- shell, Fg 14.4, Fg 15.128
- Xenophora solarioides*, 776
- radula, Fg 15.128
- Xenophoridae, Fg 14.4, Fg 15.128, Tb 15.1, 766, 776
- family treatment, 776
- ornamentation, 614
- Xenophoroidea, Tb 15.1, 766
- description, 775
- locomotion, 612
- Xenoskenea*
- in Australia, 856
- egg masses, 856
- habitat, 856
- Xenostrobus*, 251
- internal morphology, Fg 6.1
- musculature, Fg 1.13, 205
- tentacles, 251
- Xenostrobus pulex*
- habitat, 251, 253
- Xenostrobus securis*
- life span, 218
- regulation of breeding, 218
- reproductive timing, 24
- salinity tolerance, 251
- Xestoconcha*
- Ordovician, Tb 1.6
- Xylocarpus moluccensis*, 378

INDEX

- Xylochiton xylophagus*, 165, 178
 habitat, 175
Xylochitonidae, 161
Xylodiscula boucheti
 external appearance, Fg 15.181
 radula, Fg 15.181
Xylodisculidae, Fg 15.181,
 Tb 15.1, 856
 family treatment, 858
Xylophaga, 374, 376
 external appearance, Fg 8.50
 secondary sexual characters, 214
 settlement/habitat, 218
 shell, Fg 8.50
Xylophaginae, 371, 376
Xyloredo, 376
 external appearance, Fg 8.50
 settlement/habitat, 218
 shell, Fg 8.50
- 

Yaquinabyssia, 662
Yavorskiella, 322
Yayoiacmea oyamai, 651
Yehlioceras, 489
 yellow gland, Aglajidae, 952
Yochelcionella, Cambrian, 89
Yochelcionella daleki
 Cambrian, Fg 1.97
Yochelcionella ostentata
 Cambrian, Fg 1.97
Yokoyamaia, 951
Yoldia, Tb 1.6, 240
 biology, 240
 ciliary currents, Fg 4.12
 diversity, 240
 shell/body relationship, Fg 4.10
Yoldia freytagi, as fossils, 240
Yoldia lata, shell, Fg 5.7
Yoldia limatula, feeding, Fg 5.7
Yoldia nartheca, shell, Fg 5.7
Yoldia thracaeiformis
 pallial morphology, Fg 5.7
Yoldiella, 240
Yoldiidae, Fg 4.10, Fg 4.12, 239,
 240
Yuwenia bentleyi
 Cambrian, Fg 1.97, 89
- 

Zachsia, 215
 larviparity, 374
Zachsia zenkewitschi
 dwarf males, 215
Zafra
 distribution, 829
 shell, 827
Zanclaea, 1006
 as host of *Phylliroe*, 1006
Zaptychius, as fossil, 1057
Zeacumantus, 721
Zeacumantus bivaricata
 as fossils, 722
Zeacumantus diemenensis, 721
 as fossils, 722
Zeacumantus subcarinatus, 80, 721
 feeding, 722
 introduced taxon, 593
Zeadmete kulanda
 distribution, 846
 shell, Fg 15.172
Zebina, distribution, 751
Zebittium, 712
Zeehanian, Ordovician, 92
Zeidora, shell, 671
 Zeitz, Amandus, 10
 Zeitz, Frederick, 10
- Zelippistes*, 775
 shell, 774
Zella, 827
 distribution, 829
 shell, 827
Zella beddomei, shell, Fg 15.160
Zemira
 distribution, 835
 diversity in Australia, 837
 as fossils, 837
 head-foot, 836
 shell, 835
Zemira australis, shell, Fg 15.165
Zemistephanus, Jurassic, 97
Zenatiinae, 337
 affinities, 306
 habitat, 306
Zenatina, 337, 339
Zenatina victoriae, 339
 shell, Fg 8.22
Zenatiopsis, 339
 as fossil, 306
 as fossils, 339
Zephyrinidae, Fg 16.99, 1007
 apomorphies, 1010
 diet, 938
 family treatment, 1009
Zetela, 687
Zethalia, distribution, 689
Zoila, 780, 782–784
 association with sponges, 782
 as fossils, 784
 threat of shell collection, 76
Zoila friendii, shell collection, 76
 zonation
 coral reefs, 34
 on rocky shores, 29
Zonitidae, Fg 14.27, Fg 17.22,
 Fg 17.61, Tb 1.5, 1102
 family treatment, 1104
 gonoduct fusion, 1049
 odour, 1104
Zonitoides, 1104
 radula, Fg 17.61, 1104
Zonitoides arboreus, Fg 17.22
 distribution, 1104
 feeding, 1104
 as pest species, 1056
 reproductive tract, Fg 17.61
 shell, Fg 17.61
Zonulispirinae, 850
Zooantheria, as neomenioid prey,
 151
Zoobotryon pellucidum, 992
 zoogeographical regions
 freshwater organisms, 594
 terrestrial molluscs, 594
 zoogeography, Turridae, 850
 zooxanthellae
Aeolidiidae, 1013
 and camouflage, 938
Cardiidae, 330
Doridomorphidae, 1008
 extracellular placement, 333
Glaucidae, 1013
Nudibranchia, 16, 938
 origins, 940
 oxygen elimination, 333
 photosynthetic products, 333
Phyllodesmium longicirrum, 940
Pinufiidae, 1010, 1011
 and tridacnid distribution, 335
Tridacnidae, 16, 209, 302, 332
Tridacnoidea, 302, 307, 332
 zooxanthellae, putative
Trapeziidae, 349
Zostera, 763, 951, 961, 967, 968
Zosteraceae, limpet substratum, 644
 zygobranchs, 578
Zygoceras, 772
 zygoneury, 628
Zyzyzus, 1016

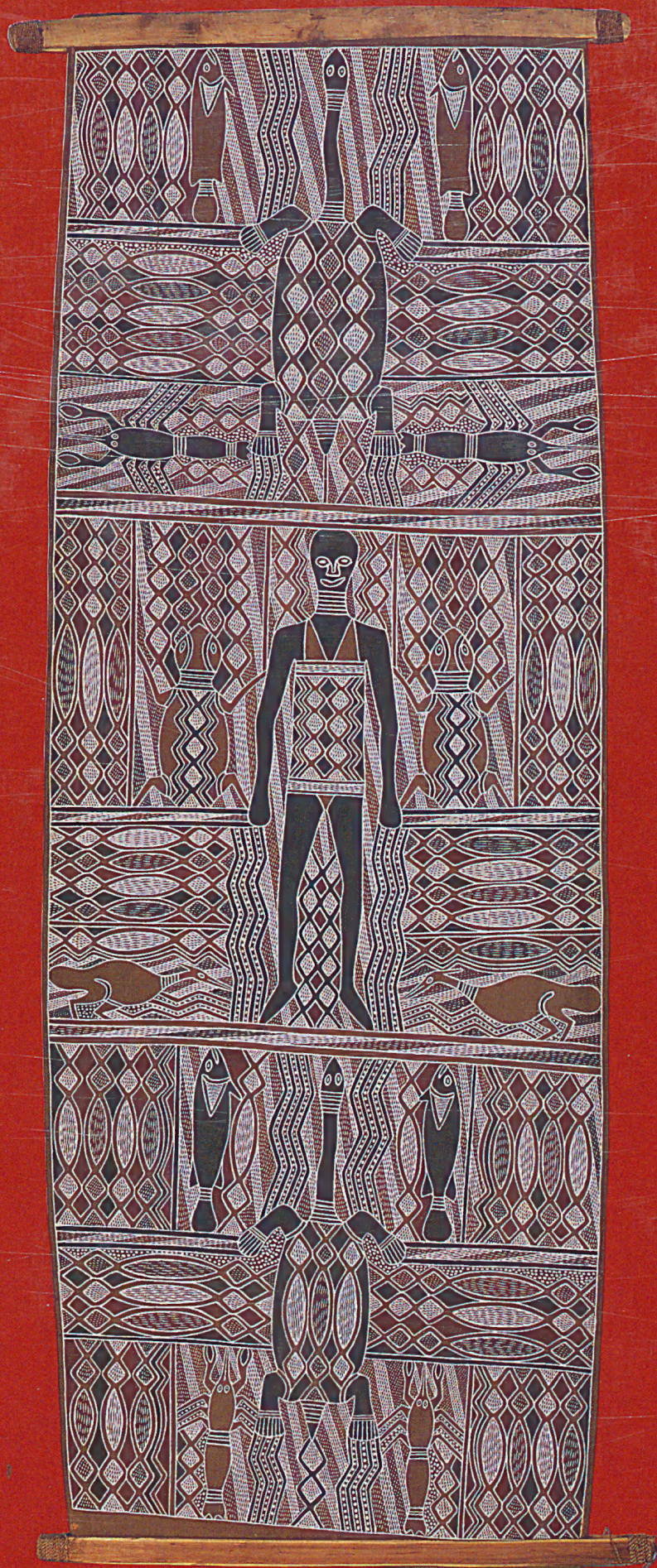






Invertebrate Department
591.95x
F264





ISBN 0-643-05756-0



9 780643 057562

